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PHYLOGENETIC TAXONOMY OF PLANTS

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TAXONOMY is the science of classification of plants and animals according to some principle, purpose, or philosophy held by the classifier. In early times men classified living things according to obvious similarities in appearance and obvious similarities in use. Many "kinds" of plants and animals were recognized and named before there was any development of real biological science and these kinds were often arranged into simple systems for the various purposes and uses to which the organisms were put.

The Emperor Shen Nung, the second ruler in the Chinese period called the "Age of the Five Emperors," was apparently the real historical "father of botany." His rule is usually dated from B.C. 2838–2698. His book is called *Shen Nung's Tree and Herb Book* and consists of three volumes. It has come down with some changes, losses, and additions, as would be expected, to the present time. It was written especially for medical purposes but also gives information in regard to food plants and industry. Besides various kinds of minerals and animals, it contains a total of 252 species of plants and these along with the minerals and animals are classified according to their supposed medicinal value or properties into three groups—1. High grade; 2. Medium grade; 3. Low grade. Later Tung Chun in the reign of Hwang Ti (2697–2513 B.C.) wrote a book of two volumes entitled *Manual for Recognizing and Collecting Medicinal Plants*. In the ancient Mosaic law the animals were grouped into various categories and these groups were then divided as clean or unclean for food. The main purpose of the classification was to distinguish animals to be used for food and ceremonial purposes from those which were to be avoided.

With the advance of biological knowledge, more elaborate and more strictly scientific systems were developed. Aristotle (384–322 B.C.) developed a classification of plants and animals which, although crude from our point of view, gave a decided impetus to the study of taxonomy. Eresios Theophrastos (370–285 B.C.) has been called the "father of botany." He described about 450 cultivated plants and classified them as herbs, undershrubs, shrubs and trees, regarding

the trees as the very highest expression of plant development. Down to the sixteenth century practically no further botanical taxonomic knowledge was developed and during the 200 years of the time of the herbalists the object of plant classification and description was still to enable interested persons to identify medicinal plants. The main interest of the herbalists in taxonomy was still about the same as it had been for Shen Nung, Tung Chun, and Theophrastos.

Coming down to modern times, the first system of plant classification that came into quite general use was Linnaeus' Artificial System, first outlined in 1735. Tournefort had established the genus concept by the year 1700 and had given definite names and descriptions to a large number of genera. In 1753 Linnaeus established the binomial system of nomenclature in his *Species Plantarum*, which has become the primary starting point for our present botanical practice in determining plant names. In this work, Linnaeus divided plants into 24 classes, 23 classes of flowering plants (Phanerogamia) and one class of flowerless plants (Cryptogamia). Within the classes, orders were recognized and the orders were divided into genera. Linnaeus recognized the fact that his system was purely artificial.

In 1789, de Jussieu developed a "Natural System" and this was a new starting point for plant taxonomy. This "Natural System" was, of course, not developed on any evolutionary principle but was nevertheless a great step in advance toward a true natural system of taxonomy. De Candolle in 1813 developed an improved system of natural classification and important additions and improvements were also made by Stephan Endlicher, Adolphe Brongniart, Alexander Braun, John Lindley, and many others, both for the higher and lower plants. In 1862–1880, Bentham and Hooker published the three volumes of the *Genera Plantarum*, with a classification which reflected many of the features of the systems of de Jussieu and de Candolle, but was nevertheless a decided improvement. The classification followed in the *Genera Plantarum* became the established system in America, through the influence of Asa Gray and others, until it was replaced in recent years by the Engler System as developed in *Die Natürlichen Pflanzenfamilien*. The Engler System of classification appeared in its first form in 1886. The Engler System is a revised and improved form of the classification of Eichler, first proposed in 1876 and further developed in later years. Wettstein has also followed the Engler System with no essential modifications. These present, standard taxonomies are regarded as true evolutionary systems but they were, nevertheless, based largely on the teleological and anarchistic theories of evolution developed by Lamarck and Darwin as well as on very superficial morphological analyses.

A new era was initiated by Bessey in developing the phyletic viewpoint of taxonomy. Bessey appropriated the best features of the Bentham and Hooker system and gradually developed a consistent phylogenetic taxonomy of the entire plant kingdom, which is more or less in harmony with our present view of the theory of descent. The germs of the Phyletic System are found in Bessey's paper, "A Synopsis of the Larger Groups of the Vegetable Kingdom," published in 1894. Bessey's system was gradually developed with many important papers on the subject until the time of his death in 1915. Among his more important contributions are papers and synopses that appeared in 1897, 1907, 1909, 1910, and 1915.

Gradually the new viewpoint began to

influence the taxonomic thinking of a few isolated taxonomists although the vast majority both in America and the rest of the world followed the Engler system without question as though it were the final consummation of all taxonomic knowledge. In 1905 Hallier published an outline of classification of the flowering plants which had many features in common with the systems proposed by Bentham and Hooker and by Bessey. In the same year the writer published his *Laboratory Outlines for General Botany* in which the study of the evolution of the flower of Angiosperms began definitely with *Sagittaria* and *Ranunculus* and ended with *Taraxacum*. In 1910, in the second edition, the magnolia was placed before these as being a more suitable type for the study of the primitive angiospermous flower. In this edition was also included a "tree" of the 16 phyletic groups, the Diatomeae and the Conjugatae being then regarded as entirely distinct phyla. From 1905 to 1922 the writer published a series of papers on "The Classification of Plants" based on the phyletic idea and a new series, "Principles of Plant Taxonomy, I-X" has been published in 1924–1931. In 1928, the author also published a *Field Manual of the Flora of Ohio* in which the Phyletic Taxonomy is consistently developed.

In the meantime, some important European contributions have been made to the subject by Arber and Parkin, by Mez with his application of serological methods to the problem of plant relationships and more recently by Hutchinson and by Schellenberg.

Botanical science has at last advanced far enough, that a rather conclusive taxonomy can be established on a true, evolutionary basis. But in order to discern the taxonomic system of plants properly, so as to avoid reasoning from the particular to the general, the botanist must certainly be familiar with the general characteristics of the whole plant kingdom, have a knowledge of life cycles, and also must be somewhat acquainted with paleontology and with ecological relations. The principle of organic change along definite lines will then become profoundly evident. On the other hand, the principle of stability is just as evident. Indeed it is so evident that, with a universal process of evolution accepted as the cause of the progression and diversity in the plant kingdom, it becomes at first difficult to realize that large numbers of plant and animal genera have remained unchanged for hundreds of millions of years. In addition to the principles of organic change and organic stability another peculiarity is in evidence. Sooner or later sexual incompatibility evolves between the members of two segregated groups and thus they become permanently isolated from each other with no further possibility of intermediates through hybridization. This incompatibility may also evolve between closely related forms. Thus completely isolated, narrow lines may be established which may continue through many geological ages, as for example *Ginkgo* and *Equisetum*.

Biological taxonomy has gone through much the same process as the classification of the chemical elements. Whereas only a few years ago the elements appeared to represent a more or less chaotic system, it now, in consequence of the new knowledge brought about through the discovery of radioactivity, appears to be such a perfect cosmos that the chemist is able to successfully predict the existence and general nature of missing elements. Although biological units are infinitely more complex than the chemical elements, the taxonomist is, nevertheless, able to postulate the necessary steps in the evolutionary

progression and actually finds such series even in the fragmentary material which is available in the living forms and the still more fragmentary material of the fossil record. He can with a considerable degree of assurance reconstruct the general characters of life forms evolved during the geological eons.

PRINCIPLES AND DICTA OF TAXONOMY

Before proceeding to the development of the phyletic system of classification, a number of the more important dicta involved in the theory of evolution and some fundamental principles, on which the author's taxonomic proceedure is based, will be presented.

1. Taxonomy is based on assumed phylogenetic relationships which come about through evolutionary processes.

2. Taxonomy must reflect a correct evolutionary theory and any evolutionary theory must itself be in harmony with a correct taxonomy. Evolution is not teleological in the sense that the structures evolved are necessarily of any special use. There is no correspondence between fundamental evolutionary movements and the taxonomic system on the one hand and the environment on the other. The same taxonomic changes take place in the most extreme differences of habitat and a change of habitat may bring no corresponding change in the taxonomic structures.

3. In developing the general system, all characteristics are taken into account,—morphological, physiological, and chemical, as also the life cycle; but so far as possible the attempt is made to define the groups in morphological terms.

4. The taxonomic characters are of different dimensions and categories. The more fundamental differences are usually the greatest and are generally unchangeable, while minute specific or varietal potentialities are less stable and their addition or loss does not disturb the fundamental system, although inhibiting or modifying factors may prevent a proper ontogenetic expression to a greater or less degree.

5. The entire taxonomic system is developed through the addition of segregative and progressive potentialities to the protoplast. In general the segregative additions are responsible for the larger and smaller phyla or phyletic lines while the progressive movements result in a more and more complex system in the individual lines as well as in the greater divergence in the characters of homologous parts. One organ or part may, however, be advancing decidedly while another remains stationary.

6. With the addition of a new potentiality old potentialities may be prevented from coming to expression entirely except in an unusual environment, or the old potentiality may be active in only a limited period of the ontogenetic cycle; thus recapitulations of ancestral activities may be evident either in the embryonic or juvenile stage, in the intermediate ontogenetic development, or at the very end of the ontogenetic cycle. Recapitulations at the end of the ontogenetic development are very common in the higher plants. These recapitulations often give definite indications of relationship. On the other hand, the new potentialities may also change the character of the embryo.

7. All of the fundamental movements which are responsible for the advancement in complexity of the taxonomic system are orthogenetic, irreversible, and mostly determinative and it is for this reason that there is a taxonomic system.

8. In the evolutionary movement there is little or no loss of fundamental potentiality acquired by the protoplast, although certain homologous parts of the

developing individual may undergo degeneration; but so-called unit characters due to Mendelian hereditary factors are often unstable and subject to loss.

9. In general, phagophytic plants are no more simple than the holophytic and may evolve into exceedingly complex systems as in some of the higher Fungi.

10. Characters or systems may come to apparent stability long before the determinate limit of the system is reached.

11. The fundamental, progressive movements have given rise to ten progressive stages which through destructive elimination have been reduced to exactly seven living subkingdoms or divisions of plants, with greater or smaller gaps between them, and each higher subkingdom always possesses all the fundamental potentialities of all the stages below it.

12. The subkingdoms, being easily delimited, determine the fundamental limits within which classes are recognized. These classes are the result of important segregative developments. Thus a class becomes: "The largest, definitely determinable, apparently monophyletic group in a subkingdom."

13. The Class is the unit of classification in the broadest sense. Classes showing a probable relationship are aggregated into Phyla, which are the largest, recognized phyletic groups. Subphyla may also be recognized, when the supposed relationship of certain classes is very obscure. On the other hand, the Classes are divided successively into smaller divisions—Subclasses (if expedient), Orders, Families, Tribes, Genera, Species and the subdivisions of these categories. The Species may be designated as Linneons containing Jordanons or varieties. Beyond these are the unit characters depending on unit potentialities or genes. Jordanons and unit characters must be distinguished from fluctuations. Polyploidy and chromosome irregularities are of little importance in taxonomy except in the problem of genetic varieties and forms and as indicating cytoplasmic disturbances brought about by past hybridizations, failure of reductions, or other abnormal chromosome reactions during karyokinesis.

14. The orders are to be limited arbitrarily and, unless an urgent reason exists, are not to exceed seven in any class, or subclass if the class is so divided.

15. In recognizing families, historical development is at present to be the primary guide, new segregations being made only in case of a very complex family aggregate. The same principle should apply to the segregation of genera and species, since the multiplication of names because of trivial differences makes the system impractical. When much division of the older groups seems advisable, the segregation can be shown by establishing subgroups, as subfamilies, tribes, subgenera, etc.

16. The fact of the accumulation of characters and the development of complexity is a guiding principle in taxonomic sequence, the simpler systems being taken first and the most complex last. Paleontology and ontogeny, when known, indicate, when properly interpreted, the proper sequence of the taxonomic series. The complexity of the system is to be judged by complexity of potentiality in the protoplast and not by mere reductions or simplifications of special parts expressed in the ontogeny. Usually a simplified organ represents a more complex reaction system than one with a greater multiplication or repetition of parts. The simpler protoplasmic units came first and the more complex evolved from them.

17. When two phyletic lines are about on a level in their lower members, the one evolving to the greater complexity at the upper limits is to be taken last. Thus the

Ferns precede the Lycopods, Pinales precede Taxales, and the Monocotyls precede the Dicotyls.

18. The details of the taxonomic system must change with advancing knowledge, but there should be no change necessary in the fundamental aspects of the system, if it is established on correct evolutionary theory.

19. The rules of nomenclature are to be determined by general international agreement; such rules should, however, not be so arbitrarily binding as to impede progress or prevent the correction of mistakes committed by the ignorance of the past. At present no final dictum should be made respecting the larger taxonomic groups.

20. The taxonomic system is to be determined by a direct appeal to the facts involved and by the free exercise of the reason, without appeal to any authority whether of high or low repute.

21. Changes and improvements in taxonomy are not to be neglected on the plea of inconvenience, and all treaties and systems not in accord with the latest established facts are to be studied only in the light of historical development.

THE TEN FUNDAMENTAL PROGRESSIVE STAGES IN THE EVOLUTION OF PLANTS

If it is assumed that all plants came from a common origin and not from a number of distinct centers of creation, then the first step in the organization of a general system of classification according to the phylogenetic principle is to make an inventory of the accumulation of the general fundamental hereditary potentialities of the protoplast from the lowest to the highest types of complexity. Such an inventory can, of course, also be made in the classification of any single phylum or smaller group. The general inventory reveals a succession of ten fundamental stages or subkingdoms, seven of which are definitely represented by known living forms.

I. Archebiophyta. The genesis of life or the transition of the first living things from the nonliving. This is assumed to have been the organization of certain types of molecules into colloidal particles of a peculiar composition or pattern which gave to these particles or autogens the fundamental and distinctive properties of living things. The original autogens were holophytic with the following properties possessed by all present autogens of living organisms. They were autonomous self-perpetuating particles which in proper conditions and surroundings reproduced their own specific composition (assimilation). They had the power of self-division, which is a characteristic property of all the organized units of higher rank in the protoplast as well as of the protoplast as a whole. They had the power of correlative interaction so that a number of the ultimate living units are held together in a limited or unitary reaction field. They had the property or power of intermittent mutation by which in isolated cases, a new pattern in one or more autogens is produced and after the mutation occurs the mutated autogen continues to reproduce only the new form by assimilation indefinitely, in some cases apparently permanently, in others until another mutation again brings a change. Aggregations of the simple uniform autogens were then the first bionts and these by intermittent mutation gave rise to bionts of various mixtures of autogens, some of which might evolve as parasites or saprophytes. Perhaps some of the disease-producing plant and animal filterable viruses are of this nature.

II. Protophyta. The second great progression and transition to a new condition of living things was caused by the organi-

zation of the more complex bionts into definite protoplasts or cells and this marks the beginning of organisms in contradistinction to the primitive bionts. The autophytic bacteria represent the lowest known stage of unicellular organisms. The organisms of this second stage are apparently entirely without sex-potentiality and mostly have a very primitive type of nucleus, typically not limited by a definite nuclear membrane and are also mostly without normally organized plastids. They evolved to the colonial and multicellular condition and to a slight degree of differentation. They evolved chloro-holophytic, saprophytic, and parasitic forms of various types, ciliated and nonciliated cells, and two chlorophyll types, a large group in which the chlorophyll is associated with a blue pigment and a small mother group with a normal, pure chlorophyll condition, a typical nucleus with nuclear membrane, and typical chloroplasts.

III. Nematophyta. The third stage in the ascending scale is the evolution of the sex potentiality with a well organized nucleus and chromosomes, giving rise to a new type of heredity (Mendelian heredity) with fertilization and reduction as normal phases in the life cycle. Several phyletic lines were now segregated, giving rise to various types of life cycles, the usual ones being the simple haploid sexual cycle, the simple diploid sexual cycle, the primitive alternation of generations cycle, and the peculiar conjugate phase cycle of the higher fungi. The lowest forms are unicellular and these soon lead up through colonial forms, mostly filamentous, to multicellular individuals with a considerable degree of differentiation. The sexual condition progresses from isogamy through various stages to typical heterogamy and finally to the condition where secondary sexual states and dimorphisms in the vegetative tissues regularly precede the formation of the hetero-gametes. The multicellular plants of this stage are mostly hermaphroditic with the unisexual condition frequently appearing in the various evolving lines. There are chloro-holophytic, parasitic, and saprophytic groups.

IV. Protobryophyta. There is an enormous break or hiatus between the living Nematophyta and the next higher stage of living plants, the Bryophyta. This break must represent a subkingdom of plants intermediate between the lower green Algae and the present lowest Bryophytes, but no such plants are known, either living or fossil. During the progression of this interval a new type of typical green plant was evolved which had a typical antithetic alternation of generations life cycle with independent gametophyte and parasitic sporophyte and with characteristic multicellular ovaries and spermaries. This typical antithetic alternation of generations life cycle is characteristic of all the higher plants and, along with other prominent characteristics, indicates that the Metathallophyta had a monophyletic origin out of the Thallophyta.

V. Bryophyta. As stated, these plants have a typical antithetic alternation of generations. The sporophyte is completely parasitic, one-phased, unbranched, and determinate in growth, the terminal bud being destroyed in the reproductive process. The gametophyte evolves in various ways, but shows two distinct stages of progression. In the lower type the archegonia are completely superficial organs, while in the highest (*Anthoceros*) the venter of the archegonium is organized from thallus tissue below the epidermis. This condition is characteristic of all the lower Pteridophyta. The sporophyte evolves from a spherical sporangium devel-

oped inside of the archegonium venter to a much more elaborate structure containing a foot, seta, hypophysis, with stomata and chlorenchyma, and sporangium. The spore tissue of the sporangium also shows a progression from the condition in which the entire center is sporogenous to a condition in which there is a completely sterile central columella. In various minor phyletic lines there is a progressive transition of the gametophyte from the hermaphroditic to the unisexual condition.

VI. Protopteridophyta. There is a prominent hiatus between the living Bryophyta and Pteridophyta. A few fossils have been found which apparently belong definitely to this gap. The fossil plants like *Rhynia*, *Hornea*, and *Psilophyton* were typical transition forms. The sporophyte had developed prominent long-continued vegetative growth and dichotomous branching but had not evolved definite roots and leaves. It had continued the terminal cauline sporangia characteristic of the Bryophytes. The fossils so far discovered apparently all belong to the Lycopod alliance.

VII. Pteridophyta Homosporae. Passing from the Bryophyta to the living Pteridophyta a number of very important fundamental potentialities are added to the reaction system. There is a change from a determinate to an indeterminate sporophyte and from a permanently parasitic condition to a parasitic phase continuing only through the juvenile period. In other words, there is a two-phased sporophyte. The reproductive process is shifted from the central or stem axis to an appendage (the leaf). Reproduction does not bring on death but the sporophyte continues to grow indefinitely through any number of reproductive periods. The gametophyte has a strong tendency to become small and short-lived. The archegonium has a short neck and its venter is imbedded in the tissue of the thallus. There is a progression from a typically hermaphroditic condition to unisexuality at the highest levels. A definite branching system is usually evolved in the sporophyte, and is either dichotomous or monopodial. A well-developed vascular system has been evolved, with a cambium layer in the fern-horsetail alliance and from this condition there is a progression to closed, scattered vascular bundles. Some phyla develop flowers (determinate, sporophyll-bearing shoots) and some continue in the flowerless condition. The sporophyte has developed roots and leaves of some sort. In the progression through this subkingdom, there is also a strong tendency to differentiate sporophylls from foliage leaves in the higher levels.

VIII. Pteridophyta Heterosporae. The most remarkable addition to the fundamental hereditary potentialities at this level is the shifting of the time of sex-determination from the ontogeny of the gametophyte to the sporophyte. In the lowest levels the determination takes place near the very end of the ontogenetic development of the sporophyte. Such a movement was, of course, already foreshadowed in the homosporous level. This shifting of the time of sex determination results in heterospory and highly dimorphic unisexual gametophytes. There is no such extreme sexual dimorphism between male and female individuals in any group of organisms as in the heterosporous plants. The gametophytes are much reduced, short-lived, and dependent on the parent sporophytes for their food supply. As in the homosporous level, some have flowers and some are flowerless. The leaves in the highest species are at least always of three types, foliage leaves, megasporophylls, and microsporophylls.

IX. Gymnospermae. Plants evolving to this level have added a large number of

new fundamental potentialities to the complement already acquired by the cell in its phylogenetic progression. The gametophytes are completely parasitic, the male gametophyte (pollen grain) becoming a two-phased parasite through the evolution of the pollen tube. The sporophyte is not only two-phased in its development but a resting phase is intercalated between the parasitic and independent phases. Along with the complete parasitism of the female gametophyte has come the evolution of the seed which is an elaborated megasporangium. Most of the phyletic lines have evolved flowers but several flowerless members are still continued, as in the living *Ginkgo* and in the carpellate plants of *Cycas*. In the highest types the inflorescence is well developed and the flower is reduced to the extreme limit. There are various progressive advances in certain phyletic lines which attain the same level as the corresponding structures in the Angiosperms, the three-celled male gametophyte for example.

X. Angiospermae. This is the culmination stage or subkingdom of the plant kingdom. The Angiosperms did not have their origin in any of the living Gymnosperm groups, but are a more advanced stage coming from the same source as the Gymnosperms, namely the eusporangiate, homosporous Ferns. The Bennettitales, which have sometimes been regarded as the point of origin for the Angiosperms, cannot be the ancestors because of the very peculiar condition of their gynecia. The Angiosperms develop their ovularies in all the hypogynous groups from the megasporophylls themselves. Nor can the Caytoniaceae be regarded as in the direct ancestral line, for they roll up their megasporophylls from the tip while the Angiosperms do so from the midrib. The Caytoniaceae and their relatives may be members of a great class or even subphylum of primitive Angiosperms. The Angiosperms have evolved a closed megasporophyll (carpel) and added a new organ, the stigma. They are all flowering plants and all the higher forms developed inflorescences, which in rare cases were reduced again to a single flower. The gametophytes are extremely reduced and the female gametophyte usually develops two sexually potential cells in addition to the single egg. At the time of fertilization of the egg, the two "polar nuclei" fuse with the second sperm and thus produce by a triple fusion an endosperm or xeniophyte. The pollen tube is a much more extensive and efficient parasite than in the Gymnosperms. There is a consistent evolution of the flower in all the phyletic lines and in many cases the extreme limit is reached in the epigynous condition. The flower progresses regularly from the primitive, strobilus-like, apocarpus, choripetalous condition to the syncarpous condition and finally to a unilocular ovulary, which condition is mostly attained at the limits whether the flowers evolve epigyny or remain in the original hypogynous state. The transition region between the vegetative parts and the sporophylls shows especially important evolutionary activities, which give rise to peduncles, involucres, generalized perianths and perianths with a specialized calyx and corolla. Such structures, aside from the peduncle, are but slightly evolved in the Homosporous and Heterosporous Pteridophytes and Gymnosperms, although a primitive perianth or involucre is sometimes present. The plant body of the Angiosperms has evolved into a great number of special types, many of which are not represented in any of the three preceding subkingdoms of vascular plants. The annuals are especially abundant. The flowers and fruits show endless developments of complex symmetries,

colors, and color patterns. The evolution of the zygomorphic flower, which appears very rarely in crude form in the Gymnosperms has been attained in many of the phyletic lines. This highly evolved complex beauty is very extreme in some lines when compared with the simple spirally symmetrical beauty of the lower flower types found in the Lycopods, Selaginellas, Horsetails, Cycads, and Conifers.

When one makes a summation of all these fundamental potentialities enumerated above for the ten successive stages and then remembers that there are many more which have not been listed, it becomes evident that the protoplast of an Angiosperm contains such a great complexity of fundamental potentialities, to say nothing of the large number of segregative group potentialities and the host of superficial unit factors or genes, that the nature of the basis for these properties in the protoplasm becomes practically incomprehensible.

THE SEVEN SUBKINGDOMS AND THE CLASSES OF LIVING PLANTS

Of the ten stages or subkingdoms enumerated above, seven are represented by the living plants of the present age, namely, Protophyta, Nematophyta, Bryophyta, Pteridophyta Homosporae, Pteridophyta Heterosporae, Gymnospermae, and Angiospermae; and with these established we are prepared to segregate the large units of classification, namely the classes. As stated in the enumeration of principles above, a plant class may be defined as the largest, definitely determinable, and apparently monophyletic group in a subkingdom. Since the subkingdoms can be definitely delimited at least in so far as living species are concerned, the class also becomes a very definite unit in developing the taxonomic system. Each class should stand for some prominent and definite character or group of characters. In establishing classes some consideration should, however, be given to the practical side of the problem. Thus about 50 definite unit groups or classes can easily be recognized and there should not be much difference in treatment between different taxonomists, provided the present definition of a class is accepted.

The segregative characters for the classes will be given below in the class synopses under each phylum, although as stated they are originally segregated within the limits of the several subkingdoms or stages. According to a liberal interpretation of the class definition, including the living classes and the well-established fossil classes, there are 29 of these groups in the Thallophyta and 22 in the Metathallophyta. These are distributed in the ten subkingdom stages as follows: Archeophyta, none definitely known to exist; Protophyta, 5; Nematophyta, 24; Protobryophyta, none known to exist; Bryophyta, 5; Protopteridophyta, 1 (fossil); Pteridophyta Homosporae, 4; Pteridophyta Heterosporae, 4; Gymnospermae, 6; Angiospermae, 2.

The classes which show a probable relationship are collected into the great phyla and of these there are about 15, with several recognized sub-phyla which some might think should be raised to phylum rank. On the other hand, the classes are the great units for subdivision into smaller and smaller groups, as stated in the outline of principles, until the species are reached, which are the general unit groups for botanical nomenclature. The criteria for these divisions are more or less arbitrary, for up to the present time no one seems to have been able to give the earmarks that would serve for a definite treatment. According to the writer's rules of procedure, the number of

orders is usually limited to seven or less for a class, or a subclass in case subclasses are necessary. According to this basis of segregation there are 200 or less well-established orders of living and fossil plants, or about an average of four per class. Many classes, of course, have but one or two orders while the most complex class, the Dicotylae, has 40 distributed among 8 subclasses. The orders now recognized as well-established groups in the author's system number 94 for the Thallophyta and 88 for the Metathallophyta. In determining the number of orders to be established in a complex class we have a problem similar to that in deciding how many large main branches a large elm tree has, for example. Of course, there are many more orders of named fossil plant remains but most of these are still imperfectly known and so cannot take their place definitely in the system at present.

The orders may be divided into suborders, if one desires to make a greater segregation before the family group is reached. Below a synopsis of the great phyla is presented and this is followed by a synopsis of the classes and subclasses in each phylum.

SYNOPSIS OF THE PLANT PHYLA AND SUB-PHYLA

I. Plant body unicellular, colonial, or multicellular, frequently filamentous; ovary when present never an archegonium; nonsexual plants or with a simple haploid or a simple diploid sexual cycle, sometimes with haploid and conjugate phases, the conjugate phase with binucleate cells; sometimes with an alternation of haploid and diploid generations, but then not of the typical antithetic type, the diploid sporophyte never having a parasitic existence or proper parasitic phase on the parent gametophyte, but originating from a free spore or zygote. (THALLOPHYTA).

A. Cells typically with poorly differentiated nuclei and chromatophores and with a primitive type of nuclear division; motile or nonmotile, with or without chlorophyll, never with a pure chlorophyll-green color; reproduction by fission; resting spores or cells commonly present. Phylum I. SCHIZOPHYTA.

B. Cells with well differentiated nuclei and if holophytic usually with definite chloroplasts; with or without chlorophyll; plants green or colorless or variously tinted by coloring matter other than chlorophyll.

(A) Unicellular saprophytic plants without chlorophyll, having a plasmodium stage of more or less completely fused cells, mostly amoeboid in nature, from which complex sporangium-like resting bodies are built up; sexuality primitive; resting spores finally liberating flagellate or amoeboid cells. Phylum II. MYXOPHYTA.

(B) Plants not developing a plasmodium, the cells usually covered with a wall during the vegetative phase.

1. Unicellular or filamentous plants containing chlorophyll, either brown and with silicious, two-valved walls or green with complex chromatophores and the walls not silicified; conjugating cells not ciliated, isogamous; with a simple haploid sexual cycle, the reduction division probably always in the zygote. Phylum III. ZYGOPHYTA.

a. With silicified cell walls and brown coloring matter. Subphylum 1. DIATOMEAE.

b. Not with silicified walls; cells green. Subphylum 2. CONJUGATAE.

2. Plants not with silicified two-valved walls nor with complex chromatophores; either nonsexual or isogamous or heterogamous; if with a direct conjugation of walled cells or branches then without chlorophyll.

(1) Plants with chlorophyll, or if without chlorophyll, then either without a true mycelium, or if a mycelium-like filament is present then with a sexual phase with ciliated, motile spermatozoids and stationary eggs.

a. Antheridium when present not consisting of a globular structure containing sperm-bearing filaments.

(a) Plants usually green, with chlorophyll or colorless, nearly all producing nonsexual zoospores; unicellular, colonial, or multicellular, nonsexual or mostly sexual plants, the sexual forms isogamous or heterogamous; nearly all with simple, haploid, sexual cycle, but some apparently with a simple, diploid, sexual cycle.

Phylum IV. GONIDIOPHYTA.

(b) Plants with the chlorophyll usually hidden by a brown, red, or purple pigment, always with a multicellular body and sexuality.

((a)) Mostly marine brown Algae with phycophaein; isogamous or heterogamous with ciliated sperms, both gametes usually discharged from the gametangia; with a simple, diploid, sexual cycle, perhaps some also with a simple, haploid sexual cycle, or in the higher forms with two or more types of the alternation of generations cycle. Phylum V. PHAEOPHYTA.

((b)) Mostly marine red or purple Algae with phyco-erythrin; heterogamous, with stationary eggs and nonciliated sperms; apparently normally with an alteration of generations. Phylum VI. RHODOPHYTA.

b. Filamentous, aquatic, green Algae with globular antheridia containing sperm-bearing filaments, the sperms being bicilated; nonsexual spores absent; with a simple, diploid, sexual cycle, the reduction division apparently taking place in the sexual organs.

Phylum VII. CHAROPHYTA.

(2) Plants without chlorophyll and with a true, septate or nonseptate mycelium; sexual reproduction without motile sperms; nonsexual reproduction of various types; with a simple, haploid, sexual life cycle, or in the higher forms with a modification of this cycle, in which a binucleate or conjugate phase follows the normal haploid phase with uninucleate cells. Phylum VIII. MYCOPHYTA.

a. Mycelium cenocytic; without ascospores or basidiospores.

Subphylum 1. PHYCOMYCETAE.

b. Mycelium normally not cenocytic; with ascospores or basidiospores, or apparently numerous degenerate forms in which such spores are no longer developed, but which are propagated solely by conidia. Subphylum 2. MYCOMYCETAE.

II. Plant body a solid aggregate; if filamentous, only so in the embryonic or immature condition; ovary a typical archaegonium or if much reduced then the plants seed-bearing; always with a typical, antithetic alternation of generations in the normal life cycle, the diploid sporophyte being parasitic during its entire life or in its embryonic phase on the gametophyte. (META-THALLOPHYTA).

A. Without vascular tissue; sporophyte parasitic on the gametophyte during its entire life and determinate in growth; homosporous; small plants without roots or true leaves. Phylum IX. BRYOPHYTA.

B. Always with vascular tissue in the sporophyte which becomes an independent plant, after the embryonic phase, with roots and leaves except in a few degenerate forms; and always with decidedly indeterminate growth of all or part of the axes.

(A) Sporophyte not seed-producing; sperms breaking out of the antheridium to enter the necks of the archegonia directly; homosporous or heterosporous, the sex being determined either in the gametophyte or in the sporophyte.

1. Spermatozoids comparative large and multiciliate; sporophylls not in cones, or in cones (strobili or primitive flowers), but then the sporophyte with jointed stems and whorled leaves; branching normally monopodial.

a. Stems not jointed, the leaves usually large and compound and spirally arranged, rarely in whorls, sporophylls never in cones, the reproductive axes always indeterminate.

Phylum X. PTENOPHYTA.

b. Stems jointed and fluted, bearing whorled leaves, which in living forms and in most fossil forms are much reduced; sporophylls in cones; living species, and many fossil forms also, some with determinate vegetative branches. Phylum XI. CALAMOPHYTA.

2. Spermatozoids small, biciliate; leaves of the living species small, covering the continuous stem in spirals, or sometimes in opposite arrangement; rarely with a slight internodal development; branching of the stem dichotomous, the lowest species all indeterminate; sporophylls usually in cones or in the lower forms in zones alternating with the sterile leaves; frequently also with determinate vegetative branches; the lowest fossil species with terminal cauline sporangia. Phylum XII. LEPIDOPHYTA.

(B) Sporophyte producing seeds, the female gametophyte always parasitic in the megasporangium (ovule) during its entire life, the male gametophyte developing a pollen-tube through which the sperms are discharged, hence with a two-phased parasitic growth, the first stage in the microsporangium, the second in the ovule, or in the higher groups beginning in the tissues of the megasporophyll itself (carpel); with a resting stage intercalated between the two phases of the sporophyte; always heterosporous, the sex being determined in the sporophyte.

1. Carpels open, without stigmas or true ovularies, the ovules and seeds naked and the pollen-grains (male gametophytes) falling directly into the micropyle; no true endosperm or xeniophyte present.
   a. Sperms so far as known ciliated and motile; ovules with a pollen-chamber; with or without flowers; the sporophylls either being in cones, or in rosettes on indeterminate axes. Phylum XIII. CYCADOPHYTA.
   b. Sperms without cilia; ovules without pollen-chambers; sporophylls in cones, which may be highly specialized or reduced and in the highest types collected into definite inflorescences; woody plants, monecious or diecious. Phylum XIV. STROBILOPHYTA.
2. Carpels or the set of carpels closed at maturity, with stigmas and with ovularies enclosing the ovules and seeds; pollen-grains falling on the stigma and developing long pollen-tubes; flowers well developed, commonly with a perianth, often highly specialized or reduced; true endosperm or xeniophyte normally present. Phylum XV. ANTHOPHYTA.

SYNOPSES OF THE CLASSES AND SUBCLASSES OF THE SEVERAL PHYLA

Phylum, SCHIZOPHYTA. About 2,500 species

I. Cells without chlorophyll, sometimes with bacterio-purpurin; holophytic, saprophytic, or parasitic Fungi.
   A. Cells not imbedded in a pseudo-plasmodium; life cycle not with distinct, vegetative and fruiting periods; not forming a myxomycete-like fructification, although the cells may be in gelatinous masses. SCHZOMYCETAE. Bacteria.
   B. Cells in a pseudo-plasmodium; life cycle with two distinct periods, a vegetative period and a fructification period, when a myxomycete-like fruiting body is developed with or without a stalk. MYXOSCHIZOMYCETAE. Slime Bacteria.

II. Cells containing chlorophyll and phycocyanin; Algae usually of a blue-green or brownish color.
   A. Without a definite nuclear membrane and with a low type of chromatophore. CYANOPHYCEAE. Blue-green Algae.
   B. With nuclear membrane and highly differentiated chromatophores; unicellular or in colonies. GLAUCOCYSTEAE. Higher Blue-green Algae

Phylum, MYXOPHYTA. About 350 species

I. Without zoospores; the cells not fusing into a typical plasmodium; but simply aggregated; spore mass without a covering. ACRASIEAE. Primitive Slime Molds.

II. With zoospores containing a single flagellum; plasmodium of completely fused cells. MYXOMYCETAE. Slime Molds.
   A. Spores developed superficially upon erect branching sporophores, no sporangia being produced. Subclass, CERATIOMYXEAE.
   B. Spores developed within a sporangium-like body with a wall, the sporangia distinct or united into an aethalium. Subclass, MYXOGASTERAE.

Phylum, ZYGOPHYTA. 8,000 species

I. Cell walls impregnated with silica, composed of two valves. Subphylum and class, DIATOMEAE. Diatoms

II. Cell walls without silica but with abundant development of gelatinous pectose, causing the plants to be slimy to the touch. Subphylum and class, CONJUGATAE.

FIG. 1. PHYLOGENETIC TREE OF THE CLASSES AND SUBCLASSES OF PLANTS

Phylum, GONIDIOPHYTA. 2,000 species

I. Plants unicellular or colonial, not truly filamentous.

A. Nonsexual, unicellular or colonial Algae without zoospores, commonly with autospores; cells normally with one nucleus. AUTOSPORAE. Primitive Green Algae.

B. Sexual primitive, parasitic or occasionally saprophytic, aquatic or aerial Fungi; or perhaps some nonsexual. ARCHEMYCETAE. Primitive Fungi.

C. Isogamous or heterogamous, sexual Algae or probable derivatives from them, with zoospores.

1. Unicellular or colonial Algae, usually with one nucleus in each cell, rarely cenocytic, the colonial forms not produced by the symmetrical aggregation of free zoospores; vegetative stage non-motile or active; isogamous or heterogamous. CHLOROCOCCAE.

2. Algae consisting of colonies of peculiar form, becoming cenocytic, new colonies being produced by the definite arrangement of daughter cells developed in the parent cenocyte; isogamous, aquatic. HYDRODICTYEAE.

II. Green Algae or aquatic Fungi with a filamentous or massive body and 1, 2, 4, or many cilia on the zoospores and gametes.

A. Cenocytic; septate or nonseptate, isogamous or heterogamous.

1. Algae usually pure green in color.

a. Vegetative body usually septate, consisting of a series of cenocytes; chloroplasts forming a net, rarely in separate plates. SIPHONOCLADEAE. Lower Tube Algae.

b. Vegetative body usually nonseptate, with distinct, lenticular, oval, or plate-like chloroplasts. SIPHONEAE. Higher Tube Algae.

2. Filamentous, saprophytic, aquatic Fungi with stationary eggs and uniciliated spermatozoids. MONOBLEPHARIDEAE.

B. Algae having normal vegetative cells with one nucleus, with a conjugation of free-swimming gametes, or with motile sperms and stationary eggs. CONFERVEAE. Confervas.

Phylum, PHAEOPHYTA. 1,130 species

I. Zoospores, when present, and ciliated gametes with two flagella; if with an alternation of generations, then the gametophyte minute.

A. Gametangia plurilocular; zoospores produced in unilocular sporangia; apparently without an alternation of generations. PHAEOSPORAE. Little Kelps.

B. Gametangia unilocular or unicellular; zoospores none, or when present produced in unilocular sporangia and giving rise to minute male and female gametophytes.

1. With a simple diploid sexual cycle and without zoospores; gametangia unilocular; eggs large and non-motile, but discharged from the oogonium; sperms minute and free-swimming. CYCLOSPORAE. Rockweeds.

2. With an alternation of generations; nonsexual zoospores produced in unilocular sporangia and giving rise to small male and female gametophytes; gametangia unicellular; sporophyte often very large. LAMINARIEAE. Giant Kelps.

II. Nonsexual spores non-motile; sperms with one flagellum; reproductive organs external; with a regular alternation of prominent sexual and nonsexual generations. DICTYOTEAE.

Phylum, RHODOPHYTA. 3,100 species

I. Nonsexual reproduction by single thallus cells, trichogyne imperfectly developed; no pits between the thallus cells. MONOSPORAE.

II. Nonsexual reproduction by tetraspores usually developed in groups of four; trichogyne well developed; cells protoplasmically connected through large pits in the walls. FLORIDEAE.

Phylum, CHAROPHYTA. 160 species

One class, CHAREAE. Stoneworts.

Phylum, MYCOPHYTA. About 60,000 species

I. Plants with cenocytic mycelium, without or with transverse septa.

Subphylum, PHYCOMYCETAE. Algal Fungi.

A. Sexual spores, "zygospores," produced by the union of the contents of two similar or nearly similar conjugating branches of the mycelium, the one branch not penetrating the other; nonsexual spores rarely zoospores; saprophytes or animal parasites, a few parasitic on other plants. ZYGOMYCETAE.

B. Sexual spores, "oospores," formed by the union of the contents of two conjugating branches of unequal size, the smaller usually penetrating the wall of the larger by means of a fertilization tube; nonsexual spores either zoospores with one or two cilia or conidia; plant or animal parasites or saprophytes, sometimes aquatic. OOMYCETAE.

II. Plants with a septate mycelium, the vegetative cells containing one or two nuclei; normally with a conjugate phase in the life cycle. Subphylum, MYCOMYCETAE. Higher Fungi.

A. With ascospores, commonly 8 in an ascus; conjugate phase present, but usually not prominent. Here are also included all conidial types whose perfect stages are supposed to be ascomycetous.

(A) Asci developed after the conjugation of two cells of the mycelium or parthenogenetically (?); occasionally fertilization by means of detached conidia-like spermatia; nonsexual conidia usually produced; saprophytes or parasites on plants or animals, with an ordinary mycelium; many Lichen-fungi; in many species only the conidial form known. ASCOMYCETAE. Sack Fungi.

1. Ascus stage known, conidial stage also commonly present.

(1) Asci not in a definite fruiting body, with a variable number of spores or with a definite number. Subclass PROTOASCOMYCETAE. Lower Sack Fungi.

(2) Asci with a definite number of spores, in typical cases commonly 4 or 8, the asci collected on or in an ascocarp.

a. Asci arranged at different levels in the fruiting body or fasciculate and surrounded by a spherical, cylindrical, pyriform, or shield-like wall which is commonly perforated at the top, but sometimes completely closed.

(a) Asci arranged at different levels in the fruiting body; or the hymenium lining cavities; mostly mold-like or tuber-like Fungi. Subclass, PLECTOMYCETAE. Little Tuber Fungi.

(b) Asci in fascicles arising from a common level in a perithecium or cleistothecium or under a shield-like wall; mostly dark-colored Fungi. Subclass, PYRENOMYCETAE. Black Fungi.

b. Asci collected in a flattened, concave, convex, or irregular hymenial layer or the asci permanently enclosed; fruiting body (ascoma) a disk-like or cup-like apothecium or at first closed and opening at maturity, the hymenial layer sometimes becoming pulverulent; sometimes prominently stalked. Subclass, DISCOMYCETAE. Disk Fungi.

2. Ascus stage not known, the hyphae bearing conidia only, also isolated conidial stages whose asci are known; imperfect Fungi with the conidia superficial or in pycnidia, borne on loose innate hyphae. A provisional subclass for conidial forms with uninucleate cells. Subclass, DEUTEROMYCETAE. Imperfect Fungi.

(B) Asci developed after fertilization by means of a trichogyne and spermatium, no conidia known, but the spermatia sometimes conidium-like; minute Fungi with a peculiar vegetative body parasitic on various insects, especially water beetles. LABOULBENIAE. Beetle Fungi.

B. With basidiospores, commonly 4, developed on a basidium, one prominent stage of the mycelium with two nuclei in each cell (conjugate phase) and with clamp connections in some groups; conidia sometimes produced, or spores of various types.

1. Basidia arising from teliospores; often other types of spores also produced; plant parasites, often heterecious; conjugate phase often prominently developed. TELIOSPORAE. Brand Fungi.

2. Basidia produced directly on the vegetative mycelium, no proper teliospores being present, mostly saprophytes, but some parasitic, especially on trees; often with massive and very complex fruiting bodies; conjugate phase prominently developed, with clamp-connections; terrestrial or epixylous; a few Lichen-Fungi. Here are included the most if not all of the sterile mycelia known as mycorrhiza. BASIDIOMYCETAE. Basidium Fungi.

a. Basidia septate transversely or longitudinally, or sometimes merely deeply two-forked; fruiting body mostly gelatinous; saprophytes. subclass, PROTOBASIDIAE.

b. Basidia nonseptate.

(a) Basidia on a distinct, membranous hymenium exposed from the beginning or at first covered but finally naked, covering gills, pores, spines, or a smooth or wrinkled surface; rarely parasitic and without a special fruiting body, the basidia then arising out of the epidermis of the host plant. Subclass, HYMENOMYCETAE.

(b) Basidia enclosed within a definite peridium but sometimes exposed at maturity, the spores then borne in a more or less deliquescent gleba. Subclass, GASTEROMYCETAE.

Phylum, BRYOPHYTA. 17,000 species

I. Gametophyte with gametangia not imbedded in the thallus tissue; sporophyte not with intercalary growth between the sporangium and foot; sporangium not two-valved when a central columella is present.
A. Rhizoids unicellular; mature gametophyte thalloid or a stem-like frond with scales; sporangium without a central columella, without or with elaters. HEPATICAE. Liverworts.
B. Rhizoids multicellular or septate; mature gametophyte not thalloid; nearly always stem-like and covered with scales; sporangium nearly always with a central columella, if not, then without elaters.
1. Gametophyte with a pseudopodium bearing the mature sporophyte; sporangium not with a complete columella, but with a dome-shaped cavity.
a. Gametophyte gray-green, with two kinds of cells in the scales, narrow ones with chlorophyll and large ones without, but commonly with spiral fibril bands; sporangium with an operculum. SPHAGNEAE. Bog Mosses.
b. Gametophyte dark colored, not with two distinct kinds of cells in the scales; sporangium splitting into 4 or more valves. SCHIZOCARPAE. Granite Mosses.
2. Gametophyte without a pseudopodium; sporangium nearly always with a complete columella, usually with an operculum and a well-developed peristome of teeth. ODONTOCARPAE. Mosses.
II. Venter of the archegonium sunken in the body of the gametophyte; rhizoids unicellular; sporophyte with prominent intercalary growth between the sporangium and foot; sporangium two-valved, with a central columella. ANTHOCEROTAE. Hornworts.

Phylum, PTENOPHYTA. 7,000 species

I. Sporophyte homosporous; gametophyte usually comparatively large and mostly hermaphroditic except in extreme forms. PHYLLOPTERIDAE. Ferns.
A. Sporangia eusporangiate in origin. Subclass, EUSPORANGIATAE.
B. Sporangia leptosporangiate in origin. Subclass, LEPTOSPORANGIATAE.
II. Sporophyte heterosporous; gametophytes minute, unisexual; leaves not with ligules; sporangia in sori inclosed in a modified leaflet (sporocarp) or in modified indusia; leptosporangiate. HYDROPTERIDAE. Water Ferns.
III. Sporophyte heterosporous; gametophytes minute, unisexual; leaves with ligules and with sporangia borne singly, imbedded on the upper side near the base; eusporangiate. ISOETEAE. Quillworts.

Phylum, CALAMOPHYTA. 23 living species

I. Sporophyte homosporous; gametophytes hermaphroditic or the highest somewhat unisexual.
A. Leaves not fused into a sheath; sporangia stalked on the upper side of the sporophyll; stem with a central, triarch vascular bundle; paleozoic fossils. SPHENOPHYLLEAE.
B. Leaves united into a sheath with teeth; sporophylls shield-shaped, with sack-like sporangia on the inner side; stem with a ring of vascular bundles and a central pith which is usually hollow, some fossil forms with secondary thickening. EQUISETEAE. Horsetails.
II. Sporophyte somewhat heterosporous; gametophytes unisexual; paleozoic fossils. CALAMARIAE.

Phylum, LEPIDOPHYTA. 800 living species

I. Sporophyte homosporous; leaves when present without a ligule; gametophytes usually hermaphroditic.
A. Sporangia large, terminal, cauline structures; Devonian fossils. ACROTHECAE.
B. Sporangia on sporophylls or in the axils of leaves. LYCOPODIEAE. Lycopods.
II. Sporophyte heterosporous; leaves with a ligule, gametophytes unisexual, small. SELAGINELLEAE. Selaginellas.
A. With increase in thickness of stem by means of a cambium; paleozoic fossil trees. Subclass, SIGILLARIEAE.
B. Without increase in thickness of stem; present day herbs. Subclass, EUSELAGINELLEAE.

Phylum, CYCADOPHYTA. 90 living species

I. Leaves usually compound; stem an unbranched shaft or with few branches.
  A. Megasporophylls only moderately or slightly differentiated from the foliage leaves; leaves fern-like, often very much compounded; no cones known; paleozoic fossils. PTERIDOSPERMAE.
  B. Megasporophylls (carpels) highly specialized, usually very different from the foliage leaves; at least one kind of sporophylls in cones, the cones bisporangiate or monosporangiate; some living and numerous fossil forms. CYCADEAE. Cycads.

II. Leaves usually simple or lobed; venation dichotomous or parallel; stems with several or numerous branches forming a crown.
  A. Without dwarf branches; leaves usually elongated with parallel veins; fossil trees. CORDAITEAE.
  B. With thick wart-like dwarf branches and ordinary branches having well-developed internodes: leaves fan-shaped, dichotomously veined, sporophylls not in cones, the plant entirely flowerless, all fossil except one surviving living species. GINKGOAE. Maiden-hair-trees.

Phylum STROBILOPHYTA. 400 living species

I. No vessels (enlarged tracheids) in the secondary wood; wood frequently with resin ducts or cells; leaves mostly spiral, sometimes opposite or whorled; cotyledons 2–15. CONIFERAE. Conifers.

II. Vessels present in the secondary wood, wood without resin ducts; embryo with 2 cotyledons; reduced flowers in specialized inflorescences; leaves opposite or in threes. GNETEAE. Joint-firs.

Phylum, ANTHOPHYTA. 150,000 species

I. Stems with closed, usually scattered vascular bundles; embryo usually with one terminal cotyledon and a lateral plumule; flowers mostly in threes, all except the lowest types being of the pentacyclic trimerous condition or a modification of this; leaves commonly three-spiral in the lower types and two-ranked in the higher. MONOCOTYLAE. Monocotyls.
  A. Flowers with many to few free carpels, or the carpels united, in which case they are numerous, or if three, two, or apparently one, then the flowers in a spadix, usually with a spathe, or the leaves segmented and fan-like or featherlike; a few with reduced flowers in glomerules and a few aquatic plants extremely modified and without a perianth.
    1. Aquatic or mud plants, or rarely non-green phagophytes, with primitive or highly specialized flowers, but not in a typical spadix or dense glomerules; hypogynous or epigynous herbs. Subclass, HELOBIAE.
    2. Usually terrestrial plants but sometimes aquatic; trees, shrubs or herbs with segmented leaf-blades, or plants with the flowers in spadixes or dense glomerules, usually with spathes; or minute, free-floating plants without leaves and with extremely reduced flowers; hypogynous; choripetalous, sympetalous, or apetalous. Subclass, SPADICIFLORAE.
  B. Flowers with united carpels, normally pentacyclic and trimerous or a modification or reduction of this type, often covered with glumes and then having a vestigial perianth or none whatever; if trees with pentacyclic trimerous flowers then not in spadixes and the leaf blade not segmented.
    1. Flowers usually reduced, always hypogynous, in spikelets covered with glumes, the ovulary nearly always unilocular; leaves narrow and usually elongated; usually with one or all the internodes elongated. Subclass, GLUMIFLORAE.
    2. Flowers mostly showy and normally pentacyclic, or of a somewhat modified pentacyclic, trimerous type, rarely covered with glume-like structures, hypogynous or epigynous; trees, shrubs, vines, and herbs of many types. Subclass, LILIIFLORAE.

II. Stems with open vascular bundles usually in a circle, with a cambium cylinder; embryo usually with two cotyledons and a terminal plumule; flowers mostly pentamerous or tetramerous, of many diverse types from low to high, occasionally trimerous; plants of many diverse habits, trees, shrubs, lianas, perennial and annual herbs, and other forms. DICOTYLAE. Dicotyls.
  A. Mostly with hypogynous flowers, occasionally epigymous.
    1. Mostly choripetalous or apetalous, occasionally sympetalous.
      a. Mostly choripetalous and mostly not with central placentation when the carpels are united. Subclass, THALAMIFLORAE.
      b. Typically apetalous, but some choripetalous or sympetalous; mostly with central or basal placentation. Subclass, CENTROSPERMAE.

2. Mostly sympetalous, occasionally choripetalous or apetalous.
   a. Flowers pentacyclic or sometimes a reduction from this condition; carpels mostly 5. Subclass, HETEROMERAE.
   b. Flowers tetracyclic or less; carpels mostly 2, occasionally 3. Subclass, TUBIFLORAE.

B. Mostly with perigynous or epigynous flowers or with a reduced or primitive perigynous condition.
1. Mostly perigynous or a reduction from this condition, occasionally epigynous; mostly choripetalous or apetalous.
   a. Petals commonly present; flowers usually not in ament-like clusters, hypanthium mostly prominent. Subclass, CALYCIFLORAE.
   b. Mostly apetalous; flowers, at least the staminate ones, commonly in aments or ament-like clusters; hypanthium mostly inconspicuous or reduced. Subclass, AMENTIFERAE.
2. Epigynous, with or without a hypanthium; mostly choripetalous or sympetalous, occasionally apetalous.
   a. Flowers mostly choripetalous and not in umbels; epigynous hypanthium frequent. Subclass, MYRTIFLORAE.
   b. Flowers typically sympetalous, the choripetalous groups mostly with umbels; epigynous hypanthium rare; calyx often reduced, or replaced by a specialized pappus; flowers frequently in disks or heads. Subclass, INFERAE

THE SEGREGATIVE AND PROGRESSIVE MOVEMENTS IN THE ANTHOPHYTA

The segregation of the Anthophyta into classes and subclasses has been given above and, since the flowering plants are not only the highest but also the most numerous in species and by far the most important economically, the treatment is here continued to the orders and the general phylogenetic arrangement is presented in figure 2. Since the flower is a determinate, sporophyll-bearing shoot and since there is a consistent evolution of promptness and definiteness of the determinateness of the floral axis in all the phyletic lines which evolve flowers, the results are very evident and give rise to the following general, progressive conditions: 1. Hypogynous apocarpous spiral; 2. Hypogynous apocarpous cyclic; 3. Hypogynous syncarpous plurilocular; 4. Hypogynous syncarpous unilocular; 5. Epigynous plurilocular; 6. Epigynous unilocular. These stages represent the consistent orthogenetic evolution which has resulted in the present system of flowers. As intimated the evolutionary series is dependent on the promptness of the determination of the flower axis in relation to the time of appearance of the reproductive reactions. All the lower types of flowers as represented in *Equisetum*, Lycopods, Selaginellas, Cycads, and Araucarians have spiral flowers with many free sporophylls, and in the Anthophyta the lowest types are represented by quite similar, hypogynous, spiral, apocarpous flowers, as in *Echinodorus*, *Sagittaria*, *Magnolia*, and *Ranunculus*.

Since the primitive Angiospermous flower has a regular sequence in the development of secondary sexual states, various hereditary potentialities may evolve which have an expansive effect on the floral axis in relation to the male or female state, or in some cases to both states. Thus there result finally eight fundamental, structural types of flowers, due to the evolution of the shortening of the axis and the expansions in relation to particular sexual states. Some of these types are evolved in most of the phyletic lines, which makes definition of the various subgroups very difficult. There is also an evolutionary progression from the bisporangiate flower condition through various stages and degrees of moneciousness and dieciousness. These evolutionary movements are especially responsible for many of the vestigial stamens and

carpels present in monosporangiate flowers. In many of the higher phyletic lines and occasionally in lower ones zygomorphy is evolved, which is also responsible for very definite orthogenetic series and the progressive development of vestiges and loss of parts in the flower.

When it comes to the direct question as to which of the two classes of Angiosperms represents the more primitive condition, the answer is that in some respects the Monocotyls are the more primitive and in some respects the Dicotyls. The Monocotyls have apparently in their more generalized forms preserved the primitive tree type with little branching ability, as in Palms, Dracaenas, Yuccas, Fourcroyas, and Ravenalas. The tree Ferns, and Cycads have this general form of plant body, and from this type the trees with crowns of small branches, like Ginkgoes, Araucarias, and Magnolias, have probably been derived. The Monocotyl embryo with its single terminal embryonic leaf (cotyledon) is nearer the primitive fern embryo than the Dicotyl type. The Dicotyl embryo evolved in the Cycads, lower Conifers, Gnetums, and Dicotyls. On the other hand, the ring of open vascular bundles of the Cycads, Conifers and Dicotyls is apparently a direct descendant of the vascular system of the lower Eusporangiate Ferns.

The lowest flower types among the Monocotyls are found among the Alismataceae, Cabombaceae and the lower Palmaceae, while the lowest Dicotyl flowers are present in Magnoliaceae, Ranunculaceae, and Rosaceae. Culmination types in the Monocotyls are represented by such genera as *Zostera*, *Vallisneria*, *Typha*, *Zea*, *Eriocaulon*, and *Corallorrhiza*, and in the Dicotyls by *Viola*, *Monolepis*, *Casuarina*, *Quarcus*, *Salix*, *Hippuris*, *Salvia*, *Ambrosia*, and *Leontodon*.

In the Angiosperms, bisporangiate, entomophilous flowers represent the primitive condition, from which the extreme types of entomophilous, anemophilous and hydrophilous flowers were evolved. In some of the more advanced or extreme forms, both in the entomophilous and anemophilous series, self-pollination, cleistogamy, and parthenogenesis were then evolved as extreme conditions. The lower types of flowers are usually conspicuous because of their size, while the highest are often very inconspicuous because of reduction and crowding in the evolved inflorescence, and the loss of the corolla. This may, however, be compensated by the massing of the minute flowers or the development of conspicuous involucres around the inflorescence. The apetalous Angiosperms are not primitive as suggested in the taxonomic systems of Engler and Wettstein. They are practically all reduced and syncarpous and have extremely reduced and specialized floral axes. This topsy-turvey sequence of the Angiospermous series has been a fertile source in the perpetuation of fundamentally wrong notions in regard to the evolutionary process and the causes through which evolution operates. There are several ways of determining comparative levels of development as low or high, besides the fundamental method of making a catalogue of important potentialities. The degree of divergence in structure and function of homologous parts is usually a good guide, as for example the number of diverse expressions of the same organ, as the number of types of leaves, the number of types of stems on the individual, the degree of divergence between the general vegetative axis and the floral axis or its peduncle, and the degree of divergence between sporophylls and foliage leaves.

BRIEF SYNOPSES OF THE ORDERS OF THE SUBCLASSES OF ANTHOPHYTA

HELOBIAE

I. Flowers hypogynous or somewhat perigynous, or a few epigynous; carpels free or united, spiral or cyclic.
  A. Plants normal, with chlorophyll.
    1. Hypocotylary expansion, if present, not lobed or only slightly notched; ovules usually anatropous or campylotropous; leaves often narrow, if broad, not peltate and not with a narrow basal sinus but sometimes sagittate or deeply cordate; flowers hypogynous. *Alismatales.*
    2. Hypocotylary expansion parted into two lobes or deeply notched; ovules orthotropous; aerial or floating leaves peltate or with a deep basal sinus, or if somewhat sagittate then the carpels numerous and united; hypogynous to epigynous. *Nymphaeales.*
  B. Small yellowish or reddish phagophytes without chlorophyll; tropical forest plants. *Triuridales.*
II. Flowers epigynous; carpels united, cyclic; leaves not peltate nor with a deep sinus. *Hydrocharitales.*

SPADICIFLORAE

I. Inflorescence not a typical spadix except in the higher forms; leaves frequently plicate and more or less split at maturity.
  A. Leaves usually plicate and more or less split.
    1. Carpels free or united, usually 3, forming a unilocular or plurilocular ovulary with one ovule for each carpel. *Palmales.*
    2. Carpels united; ovulary unilocular with numerous seeds on 2 or 4 parietal placentae. *Cyclanthales.*
  B. Leaves linear or sword-shaped, not plicate and not splitting at maturity; flowers monecious, spicate or capitate. *Pandanales.*
II. Inflorescence usually a fleshy spadix with or without a spathe; or minute plants without leaves, floating free, the flowers few or solitary on the modified stem. *Arales.*

GLUMIFLORAE

I. Ovulary trilocular to unilocular; ovules solitary in the cavities, orthotropous, pendulous. *Restionales.*
II. Ovulary unilocular, one-ovuled; ovules anatropous, erect or ascending. *Graminales.*

LILIIFLORAE

I. Flowers hypogynous; seeds with endosperm. *Liliales.*
II. Flowers partly or completely epigynous.
  A. Seeds with endosperm.
    1. Flowers mostly actinomorphic or slightly zygomorphic. *Iridales.*
    2. Flowers zygomorphic or very irregular. *Scitaminales.*
  B. Seeds without apparent endosperm, very numerous and usually minute; flowers mostly zygomorphic, a few of the lowest actinomorphic. *Orchidales.*

THALAMIFLORAE

I. Carpels many to one, spiral or cyclic, usually free or only slightly united; stamens usually numerous. *Ranales.*

II. Carpels usually more or less united, cyclic.
  A. Herbs with insectivorous leaves; carpels 6–3. *Sarraceniales.*
  B. Herbs or woody plants with normal leaves, not insectivorous.
    1. Carpels 2 or more, with parietal placentae, perianth, usually with an even number of segments, the flowers commonly partially or completely isobilateral. *Brassicales.*
    2. Carpels mostly 5 or 3; stamens mostly 10 or 5, or a reduction from 10, ovules mostly pendulous; flowers commonly of the hexacyclic type with one or more cycles represented by glands, or a reduction of this type. *Geraniales.*
    3. Carpels many to 3, ovules few; stamens indefinite, monadelphous, branched or clustered, or by reduction separate and few; sepals valvate. *Malvales.*
    4. Carpels 2 or more, commonly with parietal placentae; stamens numerous to few; sepals and petals usually 5, sepals imbricated or convolute. *Violales.*

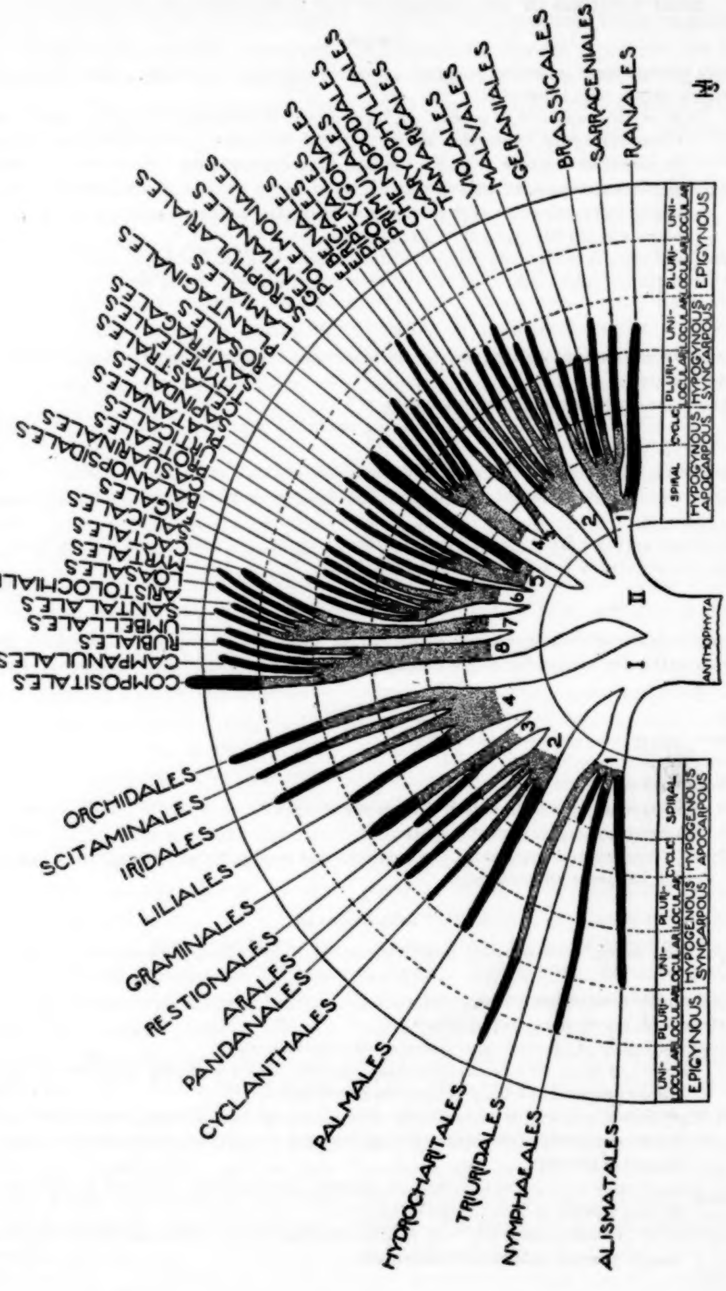

FIG. 2. PHYLOGENETIC BRANCH OF THE ORDERS OF ANTHOPHYTA

CENTROSPERMAE

I. Perianth present, consisting of a calyx and corolla, or of a calyx only.
  A. Fruit not an achene or rarely so.
    1. Corolla usually choripetalous or none.
      a. Embryo straight; fruit a capsule. *Tamaricales.*
      b. Embryo curved, coiled or annular.
        (a) Fruit a capsule, berry, or anthocarp; calyx present; corolla present or absent. *Caryophyllales.*
        (b) Fruit a utricle; calyx present; corolla usually none. *Chenopodiales.*
    2. Corolla mostly sympetalous; fruit fleshy, or a dry capsule, utricle, or achene. *Primulales.*
  B. Fruit an achene; embryo straight or nearly so; stipules commonly ocreae. *Polygonales.*
II. Perianth none or vestigial; ovules usually orthotropous. *Piperales.*

HETEROMERAE

I. Stamens mostly free from the corolla, alternate with its lobes or twice as many; seeds usually minute. flowers mostly bisporangiate, hypogynous or epigynous, sometimes choripetalous. *Ericales.*
II. Stamens united with the corolla and opposite its lobes or twice as many or more; seeds usually one or few in the cavities, usually large; flowers hypogynous or sometimes epigynous, sometimes choripetalous; *Ebenales.*

TUBIFLORAE

I. Corolla not scarious, nerved.
  A. Fruit usually a capsule, berry, drupe, or samara; carpels commonly several- to many-seeded.
    1. Corolla regular; stamens usually of the same number as the corolla lobes.
      a. Leaves alternate or opposite; ovularies not separating; carpels 3 or 2. *Polemoniales.*
      b. Leaves usually opposite; ovularies frequently separating below, with a common style; if not separating then usually with 2 cavities or 2 placentae. *Gentianales.*
    2. Corolla mostly irregular or oblique, the flowers zygomorphic, fertile stamens commonly fewer than the corolla lobes except in the lower species. *Scrophulariales.*
  B. Fruit indehiscent but usually splitting and forming 4 nutlets around the style, rarely fleshy; carpels 1–2-seeded. *Lamiales.*
II. Corolla usually scarious, nerveless; calyx and corolla 4-lobed. *Plantaginales.*

CALYCIFLORAE

I. Carpels free or united, spiral or cyclic.
  A. Endosperm usually little or none; leaves mostly with stipules; carpels spiral or cyclic, often reduced to one, usually free or only slightly united, with a few evident exceptions. *Rosales.*
  B. Endosperm present and usually copious; leaves usually without stipules; carpels cyclic, free or united, sometimes slightly epigynous. *Saxifragales.*
II. Carpels united, cyclic.
  A. Hypanthium tubular or urn-shaped, often constricted above and enclosing the ripe fruit; endosperm commonly little or none. *Thymeleales.*
  B. Receptacle developing a glandular, annular, or turgid disk which is somewhat united with the perianth or ovulary; endosperm present or none. *Celastrales.*
  C. Disk tumid, united with the perianth, sometimes reduced; endosperm usually none. *Sapindales.*

AMENTIFERAE

I. Flowers not in typical aments, often in pendent heads or ament-like spikes or clusters, usually monosporangiate.
  A. Leaves alternate or rarely opposite.
    1. Stamens alternate with the petals (when present) or numerous; perianth sometimes none. *Platanales.*
    2. Stamens commonly 4, opposite the usually 4 sepals.
      a. Calyx not petaloid. *Urticales.*
      b. Calyx petaloid; stamens usually united with the sepals. *Proteales.*
  B. Leaves whorled, reduced to scales; ovulary unilocular, with 2 ovules. *Casuarinales.*

II. Flowers, at least the staminate ones, in aments; monosporangiate.
  A. Seeds not with a tuft of hairs; fruit a typical or modified nut; achene, or samara; plants monecious or diecious.
    1. Fruit two- or several-seeded; ovules with one integument; diecious trees or shrubs. *Balanopsidales.*
    2. Fruit usually one-seeded; monecious or diecious trees or shrubs. *Fagales.*
  B. Seeds with a tuft of hairs at one end, several in the capsule; flowers normally diecious, without perianth; trees or shrubs usually with alternate leaves. *Salicales.*

MYRTIFLORAE

I. Petals usually numerous, rarely wanting; mostly fleshy, usually prickly and spiny plants with jointed stems and reduced leaves, or the stems not jointed but the leaves fleshy. *Cactales.*
II. Petals usually not more than 5 or 6 or often none; trees, shrubs, or herbs not spiny like the preceding; calyx segments rarely more than 5 or 6.
  A. Petals usually present, choripetalous, sometimes sympetalous or apetalous.
    1. Flowers mostly bisporangiate; placentae usually axile or apical, rarely basal or parietal. *Myrtales.*
    2. Flowers bisporangiate or monosporangiate; placentae usually parietal; mostly herbs or herbaceous vines. *Loasales.*
  B. Petals usually absent, if present either choripetalous or sympetalous.
    1. Ovulary usually with several cavities, usually 6; herbs or vines, sometimes parasitic. *Aristolochiales.*
    2. Ovulary unilocular; mostly parasitic shrubs or herbs. *Santalales.*

INFERAE

I. Anthers separate; trees, shrubs, or herbs.
  A. Corolla choripetalous; flowers usually in umbels or cymes. *Umbellales.*
  B. Corolla sympetalous, leaves opposite or verticillate. *Rubiales.*
II. Anthers with few exceptions united; corolla sympetalous, sometimes absent, mostly herbs, rarely shrubs or trees.
  A. Flowers not in involucrate heads. *Campanulales.*
  B. Flowers in dense involucrate heads; gynecium of 2 or rarely 3 united carpels, unilocular; seed one. *Compositales.*

THE DIRECT CUMULATIVE SERIES OF POTENTIALITIES FROM THE BACTERIA TO THE DANDELION

An inspection of the two phyletic "trees" will indicate that the Compositales have attained the highest position in the plant kingdom and in a study of this order it becomes evident that the common Dandelion (*Leontodon taraxacum* L. or *Taraxacum officinale* Weber.) belongs to the very highest type. Its direct phylogenetic history can then be reconstructed in a general way by making a summation of all the fundamental and important potentialities accumulated by its protoplast during its long evolutionary history. It will be noted that few if any of these potentialities are of the nature of the genes or unit factors with which the present science of genetics is mainly concerned. These fundamental potentialities are not added in a haphazard way, nor have they been subject to loss, at least in the surviving groups, during geological history. Genetics as at present developed and practiced is, therefore, of very little value in the more fundamental aspects of taxonomy and evolution. Its chief value at present is as an aid in the study of varieties within the species and the influence and results of hybridization between related species. With all the known mutations and hybridizations in the closely related group of *Oenothera* species, we still have an

ordinary Evening Primrose; with all the known mutations and hybridizations of *Drosophila*, we still have the little Fruit Fly. We have not made any definite progress toward an understanding of how these organisms acquired their complex complement of fundamental, progressive and digressive potentialities which determine their comparative level in the general biological scale or their relation in a certain phylum, class, order, and family. The most important fundamental hereditary properties of the Dandelion are as follows:

1. With the genesis of living things or bionts there came into existence autogens possessing the power of assimilation or self-perpetuation.

2. The potentiality of self-division, with the two daughter particles retaining all the original potentialities.

3. The power of mutation, through which from time to time an individual autogen is changed to a new pattern with new potentialities.

4. Autogens of two or more kinds with the power of correlative interaction and a number of these ultimate living units held together in a unitary reaction field.

5. The simplest unicellular condition consisting of a definitely organized reaction system or protoplast. Practically all organisms up to the highest plants and animals exist as separate cells in one or more stages of their life cycle.

6. The ordinary physiological properties or potentialities as absorption, respiration, mobility, etc.

7. Division of the organized protoplasmic units or protoplasts and their cell organs, resulting in a perpetuation of the complex system as a whole after division.

8. Property or potentiality to deposit cellulose, etc. in or on the cell wall.

9. The introduction of a more complex system of the protoplasm with highly organized nucleus, with nuclear membrane, chromosomes, etc.

10. Development of a chloroplast with chlorophyll.

11. Potentiality for karyokinesis of the higher type during cell division; with formation of a special cell wall between the daughter cells and final separation.

12. Process of photosynthesis with the usual formation of sugar, starch, etc., which is not lost in the main series.

13. Potentiality of sexuality with appearance of primary sexual states giving the property of attraction and fusion between isogamous gametes, the cells from time to time being in any of the three states,—female, male, neuter.

14. The reduction division phase with synapsis of chromosomes. The sequences of reduction, fertilization, and the individual give rise to various types of life cycles. (There is a partial inhibition of synapsis in the Dandelion.)

15. Mendelian heredity as a result of fertilization and meiosis and exhibition of dominance and recessiveness in the diploid phase. (Because of diploid parthenogenesis, no segregation of Mendelian factors usually takes place in the Dandelion.)

16. Multicellular condition, at first colonial, and a restriction of separation of cells; in the main series developing a linear aggregate.

17. Attainment of heterogamy.

18. Normal, higher type of heterogamy with extremely dimorphic gametes.

19. Differentiation system depending on physiological gradients in the multicellular body and a complexity of major and minor hereditary potentialities, not all of which are expressed at a given time or in a given cell.

20. Secondary sexual states in the gametophyte.

21. Retention of the egg in the ovary.

22. Progression from a linear aggregate to a solid aggregate, the filamentous condition being confined to the juvenile phase of the gametophyte. In the higher plants the filamentous condition is eliminated.

23. Evolution of an epidermis and distinct internal tissues.

24. Typical antithetic alternation of generations life cycle established with the twelve antithetic stages.

25. Completely parasitic, enclosed sporophyte.

26. Two-phased sporophyte, the juvenile enclosed and the mature exposed condition.

27. Transpiration established in the sporophyte, with stomata.

28. Two-phased sporophyte with parasitic and completely independent phases.

29. Indeterminate growth of sporophyte, reproduction not followed by immediate death.

30. Negative geotropism of the stem bud.

31. Central vascular strand evolved. This is shown in the embryo of the higher plants as the plerome.

32. Sinking of the archegonium venter into the tissues of the gametophyte.

33. The normal vascular system, in the main line with pith on the inside and cortex on the outside.

34. Highly evolved cambium system with secondary growth in thickness.

35. Production of lateral stem appendages or leaves.

36. Roots, originating at first as lateral organs and later as basal organs of the embryo.

37. Geotropism of roots.

38. Spiral arrangement of the lateral appendages or leaves.

39. Phototropism and decided dorsiventrality of the leaves.

40. Shifting of spore production to the leaves.

41. Monopodial branching of the sporophyte and axillary bud development.

42. Dimorphism between sporophylls and foliage leaves.

43. Shifting of time of sex determination from the gametophyte to the sporophyte.

44. In consequence of secondary sexual states in the sporophyte, dimorphic sporangia and spores produced, microspores and megaspores.

45. Unisexual gametophytes.

46. Decided reduction in size of gametophytes, namely more prompt determination.

47. Determinate reproductive axis of the sporophyte or flower potentiality.

48. Megaspore and microspore retained and germinating in the sporangia.

49. In consequence of spore retention, parasitic gametophytes.

50. Pollination process established.

51. Acquisition of a two-phased male gametophyte with development of the parasitic pollen tube.

52. Ovules or megasporangia with integuments.

53. Resting stage of embryo intercalated between the parasitic and independent phases of the sporophyte, resulting in seed dormancy.

54. Abscission of fruit or seed.

55. Sprouting of seed with complex reactions added at this phase.

56. Development of peduncle below flower.

57. Extreme differentiation of tissues of carpel and stamen from leaf tissue.

58. Closing of the carpellate leaf, producing an ovulary.

59. Development of a stigma.

60. Limitation of the growth of the gametophytes to an 8-celled female and a 3-celled male condition.

61. Preparation for triple fusion. (This is not completed in the Dandelion because of interference of new factors in the sexualization process.)

62. Triploid endosperm or xeniophyte. (Absent in Dandelion, because of failure of triple fusion.)

63. Perianth developed.

64. Change from spiral to cyclic condition of floral parts.

65. Anatropous condition of ovule from original orthotropous condition which is still repeated in the ontogeny.

66. Branching in the reproductive axis, causing an inflorescence.

67. Internodal development in sporophyte.

68. Establishment of a pentamerous condition in the flower.

69. Introduction of dicotyledonous embryo type.

70. Change to netted-veined condition of leaf from the original dichotomous condition.

71. United carpels, only the stigmas distinct.

72. Advanced determinate condition of the floral axis resulting in epigyny.

73. Sympetalous condition, from free petals, still represented by the vestigial corolla lobes.

74. Stamen characters very extreme, the anthers sagittate.

75. Union of stamen filaments with the corolla.

76. United anthers or synantherous condition.

77. Zygomorphy of corolla with split strap-shaped condition.

78. Change in internodal development, resulting in one elongated internode or scape which in favorable conditions may be over 2 feet long.

79. Rosette condition of leaves.

80. Disk or head evolved, or extremely determinate inflorescence axis.

81. Special bracts of the involucre.

82. Suppression of the leaf bracts subtending the individual flowers.

83. Unilocular ovulary with one seed.

84. Reduction of stigmas to two.

85. Coiling of stigmas.

86. Pappus development, replacing the calyx.

87. Greatly reduced flower and pedicel.

88. Development of complex leaf reaction during the ontogeny.

89. Lactiferous vessels.

90. Secretion of latex with bitter principle.

91. Hollow peduncle.

92. Hollow petiole.

93. Special root segmentation property.

94. Special reproductive property of roots.

95. Development of parachute neck at top of achene.

96. Interference with complete sexualization of chromosomes, inducing imperfect synapsis at reduction.

97. Diploid female gametophyte and parthenogenetic development of the diploid egg.

98. Interference with Mendelian hereditary transmission because of parthenogenesis.

99. Special ribs and projections on the achene.

100. Reflexing of the involucral bracts.

101. Closing of flower heads in the dark and in low temperatures.

These potentialities are all stowed away somewhere in the structure and pattern of the individual protoplast of the Dandelion. The characteristics enumerated are, of course, not always given in the order of their probable evolution but with intensive study even the approximately correct order might be discovered. It will be noted that only a few of the later potentialities are of such a nature that they might possibly be dependent on unit

genes for the characters developed. The unit gene system is apparently entirely inadequate to serve as a basis for fundamental taxonomic speculations beyond the consideration of the special varietal and specific characters, all of which can be changed without affecting the general taxonomic basis of the species or group in question. These fundamental potentialities may be due to a very complex pattern of autogens which when once evolved is never lost. They certainly cannot be due to unit genes having a definite position in a certain chromosome; otherwise we would have to assume a stability to the chromosome mechanism entirely contrary to the observed facts of chromosome behavior.

PHYLOGENETIC SERIES FROM BACTERIA TO INDIAN CORN

Indian Corn (*Zea mays* L.) represents a culmination type in the Glumiflorae of the Monocotylae. It has, like many other culmination types, a number of very extreme and bizarre characters. In the old classifications still in use the grass series has been completely topsy-turvy and in consequence taxonomists, evolutionists, and geneticists have developed entirely false conceptions and principles in relation to this most important group of plants. The lowest grasses are the bamboos with large, fleshy fruits and the highest are such types as Teosinte and Indian Corn. The first 67 fundamental potentialities enumerated above for the Dandelion are also contained in the protoplast of Indian Corn, except that there is no interference with the normal sexual processes. Continuing the series along the phylogenetic line of *Zea*, the accumulation of fundamental, progressive and segregative potentialities will be as follows:

68. Evolution of a closed, scattered vascular bundle system. This may have occurred quite early in the phylogeny of the Monocotylae.

69. Evolution of the trimerous, pentacyclic flower type.

70. Change to a characteristic, parallel-veined leaf from the dichotomous type.

71. Development of a prominent leaf sheath.

72. Union of the three carpels in the flower.

73. Change from the 3-spiral to the 2-ranked vegetative leaf condition.

74. Development of a characteristic spikelet in the inflorescence.

Beginning of the Grass Series with Bamboos, Like Ochlandra or Melocanna

75. Loss of the outer perianth cycle. The condition of the perianth in the lower groups of the Sedge Family indicates that the original grass perianth was dicyclic.

76. Addition of a contraction potentiality active in the base of the flower, resulting in a two-keeled palet.

77. Definite establishment in the grass series of 6 stamens in the flower and 3 definite lodicules (inner perianth segments), resulting in a tetracyclic flower.

78. Potentiality for a unilocular ovulary.

79. Evolution from fleshy fruit to a nut.

80. Change from a nut to a caryopsis.

81. Reduction to 3 stamens, through the more prompt determination of the floral axis.

82. Introduction of bilateral condition in the flower, eliminating one lodicule and one stigma.

83. Several flowers in a spikelet to two flowers, through more prompt determination of the spikelet axis.

84. Evolution of potentiality for annual habit.

85. Potentiality added for development of special prop-roots.

86. A special type of embryo evolved with characteristic scutellum.

87. Paired spikelet potentiality added.

88. Tribe potentiality producing hyaline flowering glumes.

89. Progression of time of sex determination to produce extreme moneciousness, with the terminal inflorescence staminate and the lateral branches carpellate.

90. Change from scattered pairs of spikelets to spikelets in rows.

91. Introduction of husk-producing potentiality, usually in correlation with the secondary female state.

92. Potentiality for long styles or silks.

93. Development of very long pollen tube.

94. Dimorphism of vegetative stem below the two inflorescences, the internodes in the secondary female state being more or less flexuous.

95. Second flower of carpellate spikelet reduced to a vestige.

96. Complete or nearly complete suppression of vestiges of the opposite sporophylls in the flower. Such vestiges or even perfect sporophylls can easily be brought back experimentally.

97. Development of the cob with suppression of branches of the carpellate inflorescence.

98. Increase in the number of spirals of paired spikelets.

99. Induration of the cob tissues.

100. Partial equalization of the pedicels of stalked and sessile staminate spikelets. This equalization can be eliminated through proper control of the sexual states.

101. A highly unstable and mutative condition of certain characters, especially composition and color of endosperm and pericarp.

PHYLOGENETIC SERIES FROM BACTERIA TO DICTYOPHORA

Dictyophora is one of the most highly evolved genera of the gasteromycetous Basidiomycetae and below is given a summation of its phylogenetic history as indicated by a summation of the more important fundamental potentialities. The species employed is *Dictyophora phalloidea* Desv. This is a most remarkable tropical plant and has been called a "fantastic fungus flower." It has a vile odor in strong contrast to its fairy-like beauty of form, its main ornament being a long, white, bell-shaped, netted and lace-like appendage, or veil looking like a lace petticoat or crinoline. Unfortunately a lack of ontogenetic investigations on this and related species makes some of the statements uncertain. However, the general nature of the enumerated potentialities is correct.

The higher Fungi may be derived phylogenetically from holophytic, chlorophyll-less Protophyta, or what is more probable from the lower green Algae belonging to the Gonidiophyta. If we take this latter view the first sixteen potentialities will be the same as in the list given for the Dandelion and a loss of chlorophyll and chlorophyll-producing bodies is assumed.

17. Potentiality for the establishment of an original, simple, haploid sexual life cycle.

18. Loss of chlorophyll through development of new potentialities to carry on the nutritive functions.

19. Evolution of potentiality for saprophytism.

20. Change in the nature of the filament to a typical septate mycelium.

21. Change from free naked gametes to copulation between walled cells.

22. Potentiality for developing basidia with four basidiospores.

23. Introduction of a potentiality which produces an incomplete primary sexualization of the gamete nuclei causing a delay in their fusion.

24. Establishment of a binucleate or conjugate phase in the life cycle through a number of vegetative divisions of the conjugate nuclei before their final fusion.

25. Development of clamp connections in the process of conjugate divisions. The clamp connections are to be interpreted as due to secondary sexual states arising in the respective fields of influence of the plus (+) and minus (−) conjugate nuclei at the time of each division.

26. The potentiality which gives the saprophytic, vegetative mycelium a reaction to grow in a subterranean habitat.

27. The potentiality causing rhizomorph development in the mycelium.

28. The potentiality which causes a compact, egg-shaped fruiting body.

29. Complete progressive evolution of the time of incomplete primary sexualization of the conjugate nuclei to the first two nuclei of the germinating basidiospore and consequent elimination of copulation of walled gamete cells. Many of the Gasteromycetae apparently have this type of life cycle.

30. Development of a tough outer peridium.

31. Evolution of the potentiality for the development of a volva gel between the peridium and the separation layer.

32. Differentiation of a separation layer or zone between the gleba and the inner gelatinous layer of the volva.

33. Potentiality for the differentiation of the gelatinous gleba.

34. Potentiality for the differentiation of the reticulate pileus or cap.

35. Potentiality for differentiating a long, elastically expanding stipe, which breaks through the peridium and carries up the pileus and gelatinous gleba and the campanulate appendage or veil.

36. Potentiality for the polarity of the fruiting body.

37. Potentiality for differentiation of the bell-shaped, netted and lace-like, white appendage or veil.

38. Potentiality for dissolving the mycelium of the gleba into a green gelatinous mass.

39. Potentiality responsible for the shape and character of the basidiospores.

40. Potentiality causing the vile odor of the expanded fruiting body.

If the phylogenetic development is considered to be more direct with no ancestral chlorophyll-bearing stage, the tenth, twelfth, and eighteenth stages of the foregoing summation of fundamental potentialities evolved in the phylogeny will, of course, be omitted.

PHYLOGENETIC SERIES FROM BACTERIA TO SPIROGYRA REFLEXA

Spirogyra reflexa Transeau is one of the higher members of the Conjugatae and shows a much simpler differentiation system and life cycle than *Dictyophora*. The first sixteen potentialities are the same as in *Dictyophora* and in the Dandelion. These are followed by the progressive addition of fundamental properties as given below:

17. Attainment of a slight heterogamy, the one gamete being stationary and the other motile through the conjugation tube.

18. Complexity of the chloroplast pattern.

19. Development of pyrenoids.

20. Evolution of conjugation tube, the gametes never being discharged into the surrounding medium.

21. Unisexuality of the filaments, which

are slightly differentiated as female (+) and male (−).

22. Slight development of secondary sexual states, as shown by the difference between the conjugating protuberances to form the tube.

23. Shape and character of the zygospore and its wall.

24. Degeneration of three of the four reduction nuclei in the zygospore.

25. Development of aplanospores.

26. Specialization of certain cells which do not conjugate, indicating a slight differentiation into vegetative and reproductive cells.

According to the same method of analysis, one of the higher mosses has 27 fundamental potentialities in common with Indian Corn and Dandelion while an ordinary Bacterium has but 8 as compared with 16 for *Spirogyra* and *Dictyophora*.

The four examples given of phylogenetic accumulation of fundamental potentialities will show how each phyletic line with its groups of genera and species has evolved cells of greater or less complexity of reaction and that in general the greater the complement of fundamental hereditary potentialities possessed by a cell the higher the group of which it is the unit. By a careful study of the whole taxonomic system a much more perfect order of phylogenetic series can be developed and this should be done for all the main series.

In conclusion it must be emphasized that the whole taxonomic system has evolved through additions, step by step, of potentialities which when once established attain a profound stability, that many of the evolutionary movements have very definite limits, and that the segregative potentialities which give rise to phylum, class, order, family and genus limits also establish a series of continuously narrower and narrower bounds within which changes may take place, until finally no more changes are possible except in the minute potentialities or genes. Such changes of or in the genes of the geneticist take place also within the narrow group limits and do not to any extent interfere with or influence the activity of the fundamental potentialities already evolved. If they did we would not have the remarkably orderly taxonomic system or cosmos presented by the plant kingdom but a taxonomic chaos.

LIST OF LITERATURE

Arber, E. A. N., and J. Parkin. 1907. On the origin of Angiosperms. *Jour. Linn. Soc. Bot. London*, 38: 29–80.

Bentham, George, and Joseph Dalton Hooker. 1862–1883. Genera Plantarum. Three Vols.

Bessey, Charles Edwin. 1894. A synopsis of the larger groups of the vegetable kingdom. *Amer. Nat.*, 28: 63–65.

———. 1894. Evolution and classification. *Proc. Amer. Asso. Adv. Sci.*, 42: 237–351. Vice-presidential address before Section G, Aug. 17, 1893. Madison, Wis.

———. 1897. Phylogeny and taxonomy of Angiosperms. *Bot. Gaz.*, 24: 145–178.

———. 1907. A synopsis of plant phyla. *University Studies (Nebraska)*, 7 (4): 275–373.

———. 1909. The phyletic idea in taxonomy. *Science*, N.S. 29: 91–100.

Bessey, Charles Edwin. 1910. The phyla, classes, and orders of plants. *Trans. Amer. Micr. Soc.*, 29: 85–96.

———. 1915. The phylogenetic taxonomy of flowering plants. *Ann. Missouri Botan. Garden*, 2: 108–164.

Campbell, D. H. 1929. The phylogeny of the Angiosperms. *Bull. Torr. Bot. Club*, 55: 479–497.

Candolle, Augustin Pyramus de. 1813. Théorie Élémentaire de la Botanique, ou Exposition des Principes de la Classification Naturelle.

Eichler, August Wilhelm. 1875–1878. Bluetendiagramme. 2 Vols.

———. 1876. Syllabus der Vorlesungen über Phanerogamenkunde.

Engler, Adolf. 1886. Führer durch den Königlich Botanischen Garten der Universität zu Breslau.

Engler, Adolf, und Karl Anton Eugen Prantl. 1887–1915. Die Natürlichen Pflanzenfamilien.

HALLIER, H. 1905. Provisional scheme of the natural (phylogenetic) system of flowering plants. *New Phytologist*, 4: 151–162.

HUTCHINSON, J. 1926. The Families of Flowering Plants. I. Dicotyledons.

———. 1929. The phylogeny of flowering plants. *Proc. International Congress Plant Sci.*, 1: 413–421.

JUSSIEU, ANTOINE LAURENT DE. 1789. Genera Plantarum Secundum Ordines Naturales Disposita.

LINNAEUS, CAROLUS (Carl von Linné). 1735. Systema Naturae.

———. 1753. Species Plantarum.

MEZ, C., und K. GOHLKE. 1913. Physiologisch-systematische Untersuchungen über die Verwandtschaften der Angiospermen. *Beitr. Biol. Pflanzen*, 12: 155–180.

MEZ, CARL. 1925. Drei Vorträge über die Stammesgeschichte der Pflanzenwelt. *Naturwissenschaft und Landwirtschaft*, Heft 4: 1–44.

MEZ, CARL, und H. ZIEGENSPECK. 1925. Zur Theorie der Sero-Diagnostik. *Botanisches Archiv*, 12: 163–202.

POOL, RAYMOND J. 1929. Flowers and Flowering Plants.

SCHAFFNER, JOHN H. 1905–1922. The classification of plants. Twelve papers in *Ohio Nat.*, Vols. 5, 6, 9, 11, 13, 14, and *Ohio Jour. Sci.*, Vol. 22.

———. 1924–1931. Principles of plant taxonomy. Ten papers in *Ohio Jour. Sci.*, Vols. 24–31.

———. 1928. Field Manual of the Flora of Ohio and Adjacent Territory. Pp. 638. R. G. Adams & Co., *Columbus, Ohio*.

———. 1928–1933. Studies in determinate evolution, I–VII. *Ohio Jour. Sci.*, Vols. 28–33.

SCHELLENBERG, G. 1928. Beiträge zu einem phylogenetischem System der Blütenpflanzen. *Beibl. Vierteljahrsschr. Naturforsch. Ges. Zürich*, 73: 358–381.

TOURNEFORT, JOSEPH PITTON DE. 1700. Institutiones Rei Herbariae.

WETTSTEIN, R. R. 1924. Handbuch der Systematischen Botanik, 3d ed.

WIELAND, G. R. 1929. Views of the higher seed plant descent since 1879. *Science*, 70: 223–228.

THE PRIMARY FOOD SUPPLY OF THE SEA

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INTRODUCTION

IT has been just forty-one years since the classic monograph *Salpa* by Brooks was published as the second *Memoir from the Biological Laboratory* of Johns Hopkins University (Brooks, 1893). Like many another publication, this memoir contained much valuable discussion of a kind not suggested by its title. On page 147, in the chapter devoted to "Salpa in its relation to the evolution of life," is a section heading "The primary food-supply" which I have adopted as a title for this paper, deeming it appropriate because the primary food supply of *Salpa* is also fundamental to the existence of other marine animals. (See also Brooks, 1894.)

Like many other oceanic observers, Brooks was deeply impressed by the scant visibility of the multitudinous life in the sea, by the extreme prominence of predaceous animals, and by the obscurity of the basic materials necessary for their support. Contrasting the ocean with the land he says: "Our picture of the ocean is an empty waste, stretching on and on with no break in the monotony, except, at long intervals, a floating tuft of sargassum, or a flying fish, or a wandering sea-bird, and we never think of the ocean as the home of vegetable life." Referring to the vast numbers of animals in the open sea he says:

> Herring swarm like locusts, and a herring bank is almost a solid wall. In 1879 three hundred thousand river herring were landed in a single haul of the seine in Albemarle Sound; but the herrings are also carnivorous, each one consuming myriads of copepods every day. In spite of this destruction and the ravages of armies of medusae and siphonophores and pteropods, the fertility of the copepods is so great that they are abundant in all parts of the ocean, and they are met with in numbers which exceed our powers of comprehension.

Continuing, he says: "Insatiable rapacity must end in extermination unless there is some unfailing supply and as we find no visible supply in the water of the ocean we must seek it with a microscope."

Although seeming to us an early observer, Brooks was not the first to attempt to express his amazement at the boundless extent of animal populations of the sea or his interest in the more amazing provision for their sustenance. In his little book *The Ocean* published in London in 1846 Gosse (p. 153) says that in describing the "green water" of thousands of square miles of Arctic seas Scoresby "computes that within the compass of two square miles, supposing these animalcules to extend to the depth of two hundred and fifty fathoms, there would be congregated a number which eighty thousand persons, counting incessantly from the Creation until now, would not have enumerated." In their account of the Zoology of the world voyage of "La Bonite," Eydoux and Souleyet (1852, p. 84) say (free translation): "The pteropods are represented in all seas and all latitudes; indeed we find these mollusks from regions under the equator to the midst of the ice of polar seas: certain species are even so abundant in the northern seas as to form, according to some voyagers, the usual food of the whale."

A strikingly similar statement concerning pteropods is made by Thompson (1877, v. 1, p. 125). In 1882 Moseley, one of the naturalists of the Challenger expedition told the meeting of the British Association for the Advancement of Science that:

> Pelagic life then includes the inhabitants of the whole ocean waters, excluding those belonging to the bottoms and shores; that is to say the inhabitants of an area equal to nearly three fourths of the surface of the globe. . . . . In point of numbers pelagic animals probably far exceed all others existing. The extraordinary abundance of life, as seen at the surface of the ocean under certain circumstances, when the water is often discolored for miles and its strata absolutely filled with small animals, has often been described by voyagers, but can never be fully realised till it is actually witnessed. . . . . The existence of pelagic animals at all is directly dependent on that of pelagic plants.

In 1881, in a lecture delivered at the National Fishery Exhibition, Norwich, England, Huxley (1902, p. 490) says of herring "shoals" having dimensions of sixteen to twenty square miles:

> In these shoals the fish are closely packed . . . . every square mile of such a shoal, supposing it to be three fathoms deep, must contain more than 500,000,000 herrings. . . . . It is no uncommon thing to find five or six—nay, even ten or twelve—herrings in the stomach of a codfish. (*Footnote*) In 1879 rather more than 5,000,000 cod, ling, and hake, were taken by the Scottish fishermen. Allowing each only two herrings a day, these fishes would have consumed more than three thousand five hundred millions of herrings in a year.

Ryder (1882, p. 240) says:

> The remarkable fecundity of the Copepoda explains the extraordinary abundance of the free-swimming species upon the high seas, and even bays, where vast schools of these crustaceans become, in turn, the food of vast schools of herrings, menhaden and shad. . . . . The prodigious numbers of herrings and menhaden is a proof of the abundance of the minute pelagic organisms upon which, with scarcely a doubt, it may be supposed they subsist.

In the half century since Moseley, Huxley, and Ryder made their pithy comments many other able observers and writers have affirmed or expanded the material features of their statements. The following list contains the names of a number of those who have been most interesting as well as informative in their efforts to describe the abundance of life in the sea and to state some of the problems of its sustenance and maintenance: Haeckel (1890), Peck (1894), Herdman (1923), Johnstone (1908), Bigelow (1926), Gran (1912), Hjort (1912), Lohmann (1911), and Lebour (1921, 1922, 1923). In vivid portrayal of the boundless extent of life in the sea, Bigelow is at least the equal of any other writer and the wealth of material presented in his *Plankton of the Offshore Waters of the Gulf of Maine* is so far superior that his paper stands alone in its capacity for conveying to the reader an understanding of the eternal pressure of the vast populations of the sea to extend their bounds. Indeed, it is possible that Bigelow's statements as well as those of some other writers may be misleading to certain readers because of this excellence of portrayal of abundance of life in the ocean, or fertility of the sea. In his wonder at the tremendous extent of many marine populations of record, one may lose sight of the fact that a shoal of herring ten miles long and five miles wide (or ten times that size) would occupy only a little of the wide reaches of space available in the open sea. And, in reality, he cannot rightly suppose that even the largest schools remain in existence unchanged throughout the year. In other words, it should be remembered that oceanic populations do not fill all space available in their habitat all of the time. For each area closely crowded in the sea, there are vastly larger areas with thin or

negligible populations at some or all seasons of the year.

In connection with his statements which I have quoted and his phrase ("primary food supply") which I have undertaken to use, Brooks gives to the latter a meaning somewhat more comprehensive than that which I prefer. Under this designation he includes microscopic animals as well as microscopic plants, a usage which does very well for his purpose of pointing out that none of the larger animals of the sea could possibly exist without the presence in abundance of microscopic creatures to furnish sustenance for them or their prey. It suits my purpose better to confine the usage to the microscopic plants equipped with chlorophyll and capable of manufacturing carbohydrates from raw materials, the so-called synthetic organisms. Brooks (1893, p. 147) says:

> both observation and deduction force us to recognize that the most important element in the total amount of marine life consists of some half-a-dozen types of protozoa and unicellular plants, of globigerina and radiolarians, and of trichodesmium, pyrocystis, protococcus, and the coccospheres, rhabdospheres and diatoms. Modern microscopic research has shown that these simple plants and the globigerinae and radiolarians which feed upon them, are so abundant and prolific that they meet all the demands made upon them and supply the food for all the animals of the ocean.

Except for the fact that he names only a few groups of microscopic forms it might be said that Brooks includes under the term "primary food supply" the same organisms that are frequently included under the term "microplankton" (the microscopic animals and plants afloat or adrift). A somewhat longer list of such organisms was given by Haeckel (1890, p. 26) as follows:

Protophytes

1. Chromaceae. 2. Calcocyteae. 3. Murraycyteae. 4. Diatomeae. 5. Xanthelleae. 6. Dictyochese. 7. Peridineae.

Metaphytes

1. Halosphaera. 2. Oscillatoria.

Protozoa

1. Infusoria. 2. Thalamorpha. (Foraminifera.) 3. Radiolaria.

Haeckel did not indicate a list with these limits. I have simply taken the part appropriate to my discussion from his general list of plankton forms. This may not exactly coincide with that which would be selected by another but it serves to indicate approximately the limits meant by Brooks and it is not far different from that recognized by present investigators, some of whom would include bacteria and some other plant groups as well as certain othe animal groups in the microplankton. The naming would also be slightly different.

Although Brooks gives prominent place to diatoms in stating his views concerning the primary food supply of the sea he is much less emphatic than Haeckel and others in calling attention to their importance. Haeckel (1890, p. 31, free translation) says: "The Arctic Ocean often becomes transformed over wide areas by enormous quantities of diatoms into a thick, dark slime, the "black water" which constitutes the feeding ground of whales. The pteropods and Crustacea, on which these cetaceans live, feed on the diatom slime, the 'black water' of North Pole travelers." Moseley (1879, p. 566) says:

> The surface water of the open ocean is full of vegetable life. Diatoms are to be found with the surface net everywhere, and in high northern and southern latitudes they abound extremely, so as to color the ice with their *débris*, change the tint of the water, fill the towing net with slimy masses and cover the deep-sea bottom with a silicious deposit of their skeletons.

Herdman (1923, p. 312) says: "the plankton which is abundant in most seas at nearly all times must be a valuable

constituent of the food both of young fishes of various kinds and also of adult pelagic or migratory fishes such as the herring and the mackerel." He mentions two groups as having this characteristic; the copepods and the diatoms and goes on to say:

> The Copepoda (being animals) feed upon the Diatoms and other allied minute organisms. The Diatoms, being plants, are, however, able to nourish themselves and build up their bodies from the carbon-dioxide and the soluble salts and other substances dissolved in sea water. Diatoms are therefore one of the *producing* groups in the sea . . . . while Copepoda are *consumers*.

Johnstone (1908, p. 77) says: "*The Diatomaceae* are above all the most important organisms in the sea regarded from the point of view of their significance as the producers of organic substance. The diatoms are the 'pastures of the sea' and correspond to the 'grass of the fields' of the land." In 1912 Bigelow (1926, p. 431) observed in Penobscot Bay "noticeably soupy" water several miles in extent which contained diatoms of a single species, *Asterionella japonica* Cl. Gran (1930, p. 5) says: ". . . . These enormous quantities of diatoms, without doubt, are the most important food for the pelagic copepods and indirectly for the fish larvae which develop after the great spring spawning period." Phifer (1933, p. 43) says:

> Marine plants are the principal source upon which the fauna of the oceans depends for the energy necessary for existence. . . . . Undoubtedly the shore algae produce organic material forming nutritive substances for bacteria which in turn are probably consumed by small protozoa. However, the phytoplankton are directly consumed and produce organic food in much larger quantities since the areal extent of their distribution is many times greater than that of the shore forms. Of the groups in the phytoplankton, such as diatoms, dinoflagellates, algal spores, coccolithophores, the first mentioned play the major rôle in temperate seas.

Since the testimony of these and many other writers agrees with my own observation that diatoms are the most prominent and the most widely represented of any of the components of the floating plant populations of the sea I shall consider them as fairly representative of the "primary food supply" of the ocean and give to them principal attention in the following discussion.

METHODS OF INVESTIGATION

Inasmuch as the particles of the "primary food supply" are microscopic, and inasmuch as they may be found in only one, in many, or in every drop of water of hundreds of square miles in extent, or at many different depths in hundreds of cubic miles of sea water, it may be supposed that the problem of investigation is not easy. In general, Brooks' assertion "Our picture of the ocean is an empty waste" is more nearly correct so far as surface visibility is concerned than my numerous quotations to show abundance. In order for diatoms to show the "soupy" appearance at the surface noted by Bigelow (an abundance relatively rare in most localities) it is necessary for them to be present in numbers of some scores, or even hundreds, of individual cells to each drop of water. If one wishes to obtain definite information as to where and when they may be found and as to the conditions which favor or hinder their occurrence he must find some way of taking them from the water for accurate observation at the same time that he obtains records of at least a few of the conditions characterizing the water from which they are being taken. Many investigators have puzzled over the problem of reliable investigation of marine plankton (organisms existing afloat or adrift in the sea) without wholly satisfactory results (Bigelow, 1926, pp. 78 and 397) and a volumin-

ous literature has been developed dealing with efforts at its solution. A few items of history will serve to give the trend of these efforts.

Haeckel (1890, p. 1) credits his teacher, Johannes Müller, with being the first (in 1845) to make regular use of a fine meshed net for capturing small organisms by dragging it through the surface water of the sea. Such a method was essentially similar to that of catching fishes by casting a coarse net into the water and dragging it through a school of fishes, the only difference being in the size and shape of the net and of the meshes. Müller used his fine net mainly for capturing the echinoderm larvae in which he was individually interested but both he and his students noticed that large numbers of other things were caught as well. Although Müller may be said to have started the use of systematic methods for investigation of the organisms afloat or adrift in the sea (the plankton) it is generally conceded that Hensen was the one to give impetus to such usage and to give it solid and permanent standing amongst the sciences. Certainly, Hensen (1887, p. 1) was the first to propose and use the word "plankton" as a descriptive name for all of the organisms which exist afloat or adrift in the sea as distinguished from the fishes and other organisms characterized by such powers of locomotion that they are able to change locality irrespective of influences of water movements. In according outstanding prominence to Hensen's influence it should not be forgotten that his improvements in the conduct of plankton investigations were introduced at a time when interest in all lines of oceanic researches had been greatly stimulated by the work of the "Challenger" and other expeditions, and when a lively interest was developing in the productivity of the sea, particularly as related to fisheries.

Roughly speaking, Hensen conceived and developed the idea that over large areas of the sea (the North Sea in particular) the plankton existed in uniform or nearly uniform abundance from the surface to the bottom, or at least to a depth of two hundred meters. This being true, he argued, the productivity of the sea could be estimated from samples taken by drawing an accurately constructed fine net from a designated depth to the surface, his theory being that the net would catch the organisms in the whole column of water beneath an area the size of its inlet. Haeckel (1890) immediately, and many others afterwards, showed that several of Hensen's assumptions are untenable but his methods are still in use to a large extent and all authorities agree that he performed great service by his courage in attempting to obtain useful estimates of the abundance of life in the sea. So far as diatoms and similar organisms of the "primary food supply" are concerned one serious objection to Hensen's method was that no tow net was fine enough to prevent great losses of individual species and specimens through its meshes.

Lohmann (1911, 1912) was especially impressed with the escape of the extremely small creatures through the plankton net and he conducted extensive investigations to show their importance and the possibility of catching them in other ways. He discovered many new species by examining the filtering equipment by which appendicularians (themselves plankton organisms) capture their minute prey and he used a centrifuge for taking others directly from samples of sea water of known volume. By using culture methods similar to those employed for bacteria on land E. J. Allen (1919) confirmed Lohmann's showing of inadequacy of tow net methods and obtained evidence that even the centrifuge did not collect all of the smallest organisms in such a

way as to make them visible under the microscope or available for use in calculating the grand total of planktonic populations. Numerous investigators have tried using filters of different kinds (including sand, paper, and patented devices) with degrees of success more or less satisfactory for researches of definitely limited type. Under certain conditions the method of merely allowing a measured amount of water to stand for a day or two in a settling tube after adding a substance to kill all of the organisms has been found to be fairly successful in collecting them at the bottom of the tube.

In the study of plankton diatoms (the outstanding representatives of the photosynthetic "primary food supply" of the sea) it seems that modern practice in collecting follows three fairly definite different lines. First, the use of the No. 25 mill silk tow net of very fine mesh (mesh openings averaging about 0.05 mm. in diameter) which is still favored by some on the plea of convenience in spite of the known errors of its performance. Second, the centrifuging of samples of water obtained by use of closing bottles, by dipping, or by pumping. Probably Gran (University of Oslo) is making most extensive use of this method to-day, although many others employ it to a greater or less extent. Third, the use of No. 25 mill silk for filtering out the diatoms from measured quantities of water poured or drained through it. The Scripps Institution of Oceanography has made most extensive use of this method, by which it has accumulated nearly 20,000 catches of plankton diatoms since September 1919.

Quantitative treatment of collected material is sometimes volumetric, the volume being read directly from centrifuge tubes or settling tubes appropriately graduated. Less frequently a gravimetric method is used, the material being weighed after desiccation. Both of these methods have the disadvantage of including débris or unwanted material and they allow no opportunity for satisfactory estimates of relative abundance of different organisms contributing to the mass being handled. More commonly the treatment is by some form of "census taking." Typically for diatoms, a definite fraction of the catch is confined in a Sedgwick-Rafter counting cell (Rafter, 1900, p. 67; Whipple, 1914, p. 35) which holds exactly one cubic centimeter of the fluid. There a part or the whole number of the specimens in the mount is counted and used for making an estimate of the numbers in the total catch.

MARINE PLANKTON DIATOMS

In preceding pages I have quoted a number of authorities (mostly not diatomists) to support the idea that diatoms of pelagic habit are the most widely distributed in space and time, and most prolific of the plant constituents of the "primary food supply" of the sea. In addition, it may be stated that they have been investigated most extensively and continuously of any of these constituents and that the information now available which concerns the "primary food supply" deals mainly with the plankton diatoms. Therefore, it is not only appropriate to select diatoms as representative but it is also almost necessary to do so for practical reasons.

Diatoms are one-celled plants, mostly invisible to the unaided eye except where they are growing in such abundance as to make visible slimy masses on wet surfaces or in water. There color is usually a pleasing shade of brown which shows a peculiar richness when many are massed together. This color is caused by "diatomin" which covers and hides the chlorophyll green necessary to photosynthesis. They are supposed to be allied to the "Green Algae" (Conjugatae) including

the pond scums and brook silks. Their outstanding characteristic is a rigid siliceous covering fashioned on the fundamental pattern of a pill box, but so modified in many species as to bear little resemblance. The best descriptions of the group (Diatomaceae or Bacillariaceae) are given by West (1916, p. 83), Karsten (1928), Lebour (1930), and Hustedt (1930). Most botanical texts tell little about them and the encyclopedias are the best references so far as ordinary accessibility is concerned. Enthusiastic diatomists consider the sculptural designs on some of the siliceous coats of sedentary diatoms as being amongst the most beautiful things in the world (Mann, 1930), but these beauties are not so evident in most of the plankton forms, which have thinner coverings and more attenuated shapes.

Apparently the first record of observation of a diatom was by Leeuwenhoek in 1702 or 1703 (Taylor, 1929, p. 4; Pelletan, 1891, p. 11). It was a fresh water form but planktonic in habit. Seventy years later O. F. Müller found another species of similar habit, after which records began to accumulate with considerable regularity. Still, it appears that the relationships of diatoms to other organisms attracted relatively little attention until after Hensen (1887) stimulated general interest in fertility of the sea by his efforts to make accurate estimates of the densities of the different kinds of plankton populations occurring together in the ocean. Haeckel (1890), Lohmann (1912), Nathansohn (1906), Herdman (1908), and Ostwald (1903) were prominent amongst European investigators who in the next twenty years gave definite attention to plankton relationships. Of those who gave particular attention in that time to the part played by diatoms in these relationships the following were notable: E. J. Allen (1919), Cleve (1900), Gran (1912), Ostenfeld (1903), and Schütt (1896).

Although handicapped by less favorable contact with the sea and by wider separation of investigators interested in plankton researches, American interest was just as keen as that in Europe, and American activities ran concurrently with those of Europe. Indeed there is no evidence that any European observer had deeper appreciation of the dependence of life in the sea upon the microscopic organisms than is expressed by Ryder as early as 1882 (already quoted in part). Perhaps Ryder, Brooks, and Peck may fairly be regarded as representing American interest in the importance of the smaller marine organisms at about the time that Hensen was launching his investigations. In addition, Peck may be considered as a leader in America in use of the method of taking small organisms from measured quantities of sea water in an effort to calculate their abundance (Peck and Harrington, 1898).

However, up to 1919 most of the American work had been devoted to plankton animals and relatively little to plankton diatoms. In that year the Scripps Institution of Oceanography of the University of California established a series of investigations, with W. E. Allen in charge, for the primary purpose of gathering authentic information about seasonal and geographical occurrence, distribution, and conditions of abundance of plankton diatoms in the Eastern Pacific. More recently additional particular attention has been given to diatoms by certain investigators under the leadership of Gran at the Friday Harbor Marine Station of the University of Washington (Phifer, 1933) and a considerable number of discontinuous studies have been made at certain points on the Atlantic coast, notably in the Gulf of Maine region and localities near Woods Hole (Bigelow, 1926; Fish, 1925).

DIATOM RESEARCHES AT SCRIPPS INSTITUTION

In 1919, the Institution adopted as standard for collecting marine plankton diatoms the method of dipping from the sea a certain quantity of water and draining it through a small conical filter made of No. 25 silk bolting cloth (W. E. Allen, 1921). Assuming that there would be considerable losses of the smaller specimens through the meshes of 0.05 mm. diameter it still appeared that enough would be caught to give a fair index of abundance, while permitting the collection to be made quickly, easily, and with an accuracy at least as great as the accuracy of selecting a sample from the great mass of water constituting the ocean. However, the most important advantage of such simplicity of method is that it can be used under almost any conditions, thus insuring that a valuable series once begun need not be broken on its account, and also encouraging the taking of collections by reliable persons lacking in skill and training. Thus it has been possible to keep collections going daily at two Southern California piers for fourteen years and to get series of surface catches at hourly or longer intervals from several different kinds of ships under full speed at sea. The results of these diatom investigations have been given in a number of reports by W. E. Allen (1921, 1922, 1923, etc.) and his assistants. At present, it seems to be more appropriate to this discussion to confine attention to a limited number of selected topics than it would be to attempt to summarize the details of these reports.

THE PROBLEM OF UNIFORM DISTRIBUTION

One of the strangest phenomena in the history of science is the perpetuity of certain ideas, theories, or assertions after they have been shown to be untenable. One might suppose that scientific training would enable its beneficiaries to avoid this trait of humanity in general but there is considerable evidence that it does not. The history of Hensen's (1887) assumption that plankton is uniformly distributed in sea water over a wide area and to considerable depths illustrates this point. Haeckel (1890, p. 57) objected to it almost immediately. Herdman (1922) noted that even when simultaneous tow net catches are alike in quantity they may be far different in quality (in the kinds of organisms included). Bigelow (1926, p. 78) says "even a cursory examination of the zooplankton, if extended over a considerable area or through a considerable period of time, is certain to reveal wide fluctuations in abundance as well as in its quantitative composition, both from season to season and from place to place." (*Cf.* p. 403.) Many other investigators have reached similar conclusions, but even to-day there are probably considerable numbers of people who accept Hensen's assumption. The reason for this attitude may exist in the fact that Hensen qualified his assumption by saying that it would apply wherever the conditions of the water itself were uniform, a condition which is now known to be rarely found even on the surface, much less at any given level or at successive levels below the surface within the range of plankton occurrence.

Realizing that a part of the difference of opinion concerning the validity of Hensen's assumption might be due to experiences in different regions and with a view to getting a considerable body of evidence bearing on the question as related to diatoms, as well as for certain other reasons, two collecting stations (positions) were selected respectively five and ten miles off shore from the Scripps Institution pier and visited regularly for parts of seven summers in the last fourteen years. In every year it was found that there were

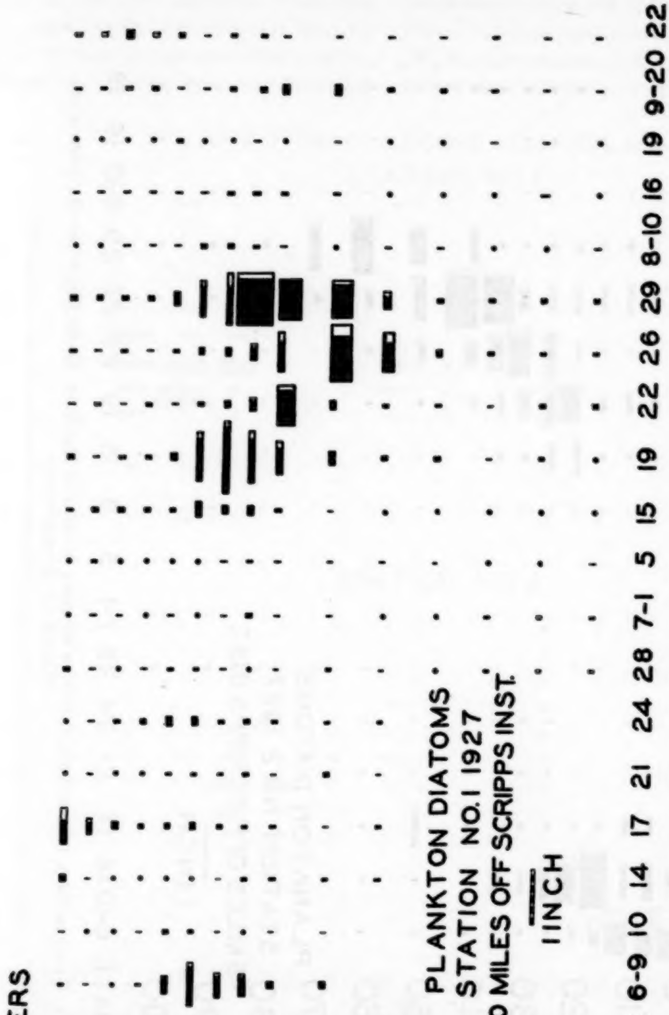

FIG. 1. GRAPH TO SHOW RELATIVE ABUNDANCE IN NUMBERS OF CELLS AT DIFFERENT LEVELS BELOW THE SEA SURFACE AT STATION 1 IN JUNE–JULY 1927

Shaded areas in rectangles represent percentage in good condition, unshaded in bad condition

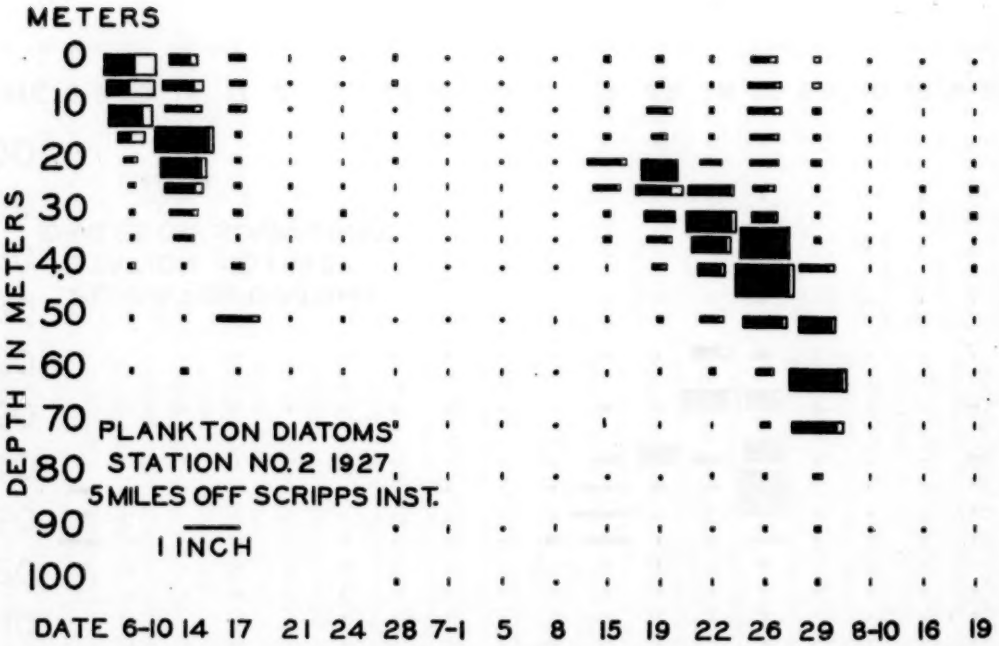

FIG. 2. GRAPH TO SHOW RELATIVE ABUNDANCE IN NUMBERS OF CELLS AT DIFFERENT LEVELS BELOW THE SEA SURFACE AT STATION 2 IN JUNE–JULY 1927

Shaded areas in rectangles represent percentage in good condition, unshaded in bad condition

considerable differences in the surface catches at the two stations, abundance being greater at the five mile station more frequently than at the ten mile station, although the reverse was true in many cases. Even in 1924 (Sleggs, 1927, p. 102) when there was an occurrence of "red water" in the area, which persisted for more than a week (showing great stability of conditions), uniformity of abundance was lacking not only at the two stations but between them and the shore. In 1926 (W. E. Allen, 1928) and again in 1927 (W. E. Allen manuscript) series of catches at five and ten meter intervals were obtained by the Allen closing bottle at both stations in which striking differences in abundance of diatoms appeared at every level, the catches at both stations being taken in the same forenoon at each time.

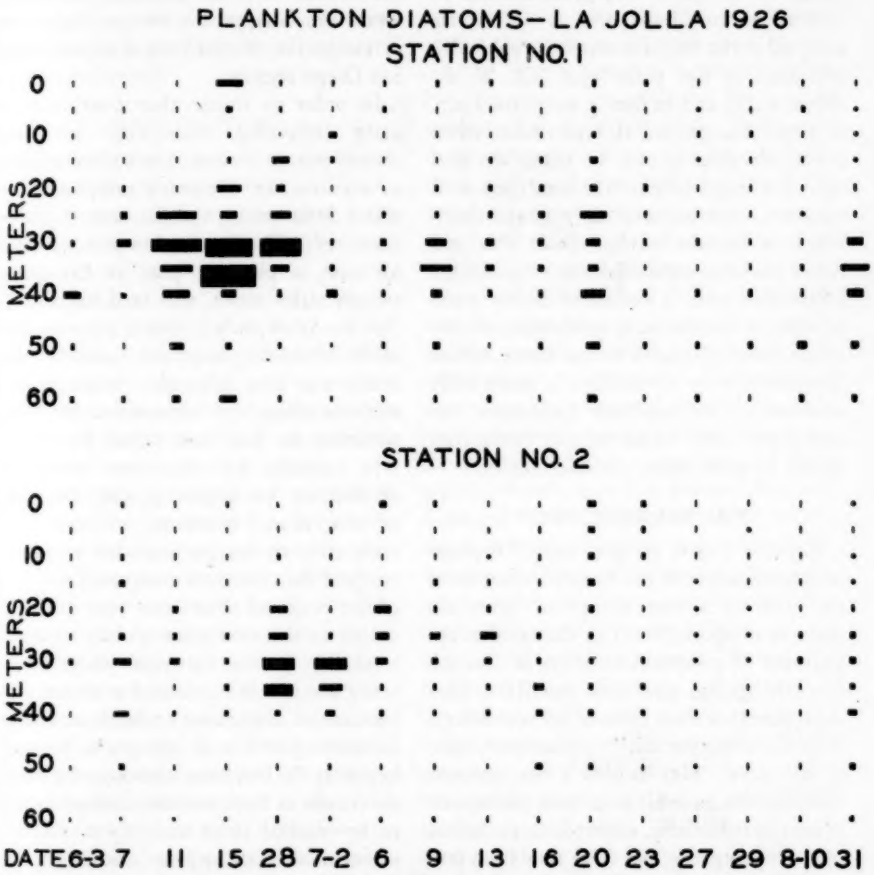

Fig. 3. Graph to Show Relative Abundance in Numbers of Cells at Different Levels Below the Sea Surface at Station 1 (10 Miles Off Shore) and Station 2 (5 Miles) in June–July 1926

Large shaded rectangles represent large numbers, smaller less

However, in these two instances the differences were in abundance rather than in constituents, the principal species at both stations being *Thalassiothrix frauenfeldii* Cl. and Grun. in 1926, and *Nitzschia seriata* Cl. in 1927. The gross features of differences in abundance at all levels sampled at the two stations are graphically indicated in fig. 3 for 1926 (*Cf.* W. E. Allen, 1928) and in figs. 1 and 2 for 1927, in which the graphs, though smoothed to a considerable extent by using decimal orders of magnitude to represent the actual numbers, show astonishingly greater abundance at certain levels. From this and other evidence accumulated by the Scripps Institution over a period of thirty years it appears certain that uniformity of distribution of plankton in sea water, either horizontally or vertically, is practically nonexistent in Southern California waters at any time, whatever may be the condition in some other oceanic locality.

SEASONAL DISTRIBUTION

Bigelow (1926, p. 465) says "Perhaps no phenomenon in the natural economy of the gulf so arrests attention (certainly none is so spectacular) as the sudden appearance of enormous numbers of diatoms in early spring, and their equally sudden disappearance from most of its area after a brief flowering period." Johnstone (1908, p. 97) says "May begins a new season. The diatoms have hitherto been prominent plankton organisms, often to the exclusion of everything else, but from now for a few months they begin to decrease in numbers." Gran (1930, p. 5) says "It is a characteristic feature of the plankton production off the coast of Norway that after the dark winter months, as soon as the light is sufficient for their photosynthesis, there is an enormous growth of pelagic diatoms." Similar comments have been made by many other observers, mostly from North Atlantic or North Sea regions. Since their latitudes are higher by distances of a thousand miles or more than those of Southern California the interest of obtaining data for comparison was added to that of learning the actual facts of seasonal occurrence when the Scripps Institution began the investigation of plankton diatoms in the San Diego region.

In order to insure that continuity of daily collecting throughout the year should not be broken, piers were selected as stations for obtaining samples of sea water from which the diatoms might be extracted. The Institution pier was used for one, a pleasure pier at Oceanside, twenty miles north, was used for another (for six years only), and a pleasure pier at Pt. Hueneme, over one hundred miles north was also selected. At all of these stations there was somewhat the same tendency as has been noted for northerly latitudes for maximum abundance of diatoms to appear in the first third of the year. However, no two years were alike in the ten years for which the study of data has been completed and most of the peaks of abundance were not coincident at the two more widely separated stations. In the ten years there was a fairly distinct indication of a tendency for increase of abundance to begin at the Institution pier five or six weeks before it began at Pt. Hueneme although the actual maximum at both stations seemed to tend to be reached in or near April, and was sometimes as late as June (once in September) at the Institution pier. The authors quoted, and most others referring to the phenomenon, attribute the vernal increase ("flowering" or "efflorescence") of the plankton diatoms to increase in light, to increase in temperature, and to surplus nutrients (accumulated in the waters in the less productive months of winter). One cannot escape the conviction that

these conditions must play a large part in accounting for the vernal increases in abundance in Southern California as well as elsewhere, but the explanation is really not so simple as that, else why should an abundance sustained near to the April maximum for some weeks appear (at the Institution only) in February of 1920 and not in other years?

YEAR DIFFERENCES

Biologists (as well as other people) not familiar with the inconstancy of unrestricted Nature might suppose that daily observations on a particular kind of organisms for a year would give a reliable understanding of the conditions of its existence in a particular locality. As a matter of fact, such a body of information may be misleading to a greater or less extent in a number of different ways, some of which are well illustrated by experiences in the Southern California region.

In a preceding paragraph I mentioned the fact that *Thalassiothrix frauenfeldii* was the most prominent diatom in boat catches for 1926. This was the only year that it has attained such prominence in Institution material. Indeed, it is inconspicuous or missing in the catches of most years. Still, any one depending on the information for that one year would feel fully warranted in saying that that particular species was a conspicuous and characteristic feature of the diatom flora of the Gulf of Santa Catalina. Other examples not quite so striking appear in the Institution records.

For the year 1920 (W. E. Allen, 1922a) the total diatoms for the year obtained by daily catches at the Institution pier were considerably larger than the total from similar catches at Pt. Hueneme. This appeared to offer good foundation for an inference that La Jolla sea water was more productive than Pt. Hueneme sea water. In 1921 (W. E. Allen, 1927) there was less difference but still a greater total abundance at La Jolla. If the records had stopped with that year the conclusion would be readily accepted anywhere that the fertility of the sea was greater at the more southerly station. But continuance of the observations showed that in succeeding years there was a reversal, with Pt. Hueneme more often in the lead in individual years of the ten. Even two years was not sufficient to give a reliable idea of the relative productivity of the two localities.

E. J. Allen (1908, p. 397) has commented on the showing of Bullen (1908, p. 269) that there appeared to be a correlation between the number of mackerel taken in May and the number of copepod food organisms in their vicinity and suggested that since the copepods depend on plant food there ought to be a further connection between the amount of sunlight in February and the abundance of plants (plankton diatoms). He examined sunshine records and such fisheries records as were available and came to the conclusion that "they indicate a fundamental correlation between the abundance of mackerel in May and the amount of bright sunshine during the earlier months of the year." Even though his conclusion be questioned, it has the important use of calling attention to the generally accepted view that sunshine in the early months of the year is favorable to diatom production, and through it to the increase of vast numbers of different kinds of animals, many in larval or immature stages of development. Assuming the reality of this relationship it is easy to understand that if the diatom increase comes late in the season of a particular year it may be too late to feed enormous populations of young animals of that year, including some of the fishes. In other words, it is not only important that

there should be adequate production of the plants but that it should come at a time of year favorable for many animals. Harvey (1928, p. 165) says:

> It cannot be assumed that where vegetable carbohydrate and protein food exist, there will be an animal population to eat a *fixed* proportion of it. Besides a supply of phytoplankton suitably spaced in time, a further condition necessary for maximum population is that the energy of plant life passed on to the plankton-feeding animals should, before they die, be handed on to the carnivorous animals.

Lacking in necessary approach to a coincidence with animal needs, plant productivity ceases to be a reliable index to fertility, and it may be that the smaller amount of one year or place is more serviceable in the economy of the sea because it is timed more appropriately than the larger amount of another year or place. Therefore, the early and sustained abundance in La Jolla Bay in 1920 may have made it superior to any other year of the ten in respect to general conditions of fertility. As a matter of fact, mackerel fishing was exceptionally good at the Institution pier that year, indicating some degree of correlation, so far as the evidence goes.

LOCALITY DIFFERENCES

Just as certain localities are known to be more favorable than others for catching marine fishes, so certain localities are known to be especially favorable for plankton organisms, including the diatoms. The great abundance of plankton organisms, including diatoms, on the Malabar Coast of India as reported by Hornell and Nayudu (1924) shows that region to be exceptionally favorable. For many years it has been known that a particular species of diatoms is to be found in astonishing abundance at a certain time of most years on Copalis Beach (near Gray's Harbor) in the State of Washington as is mentioned by Galtsoff (1932). Gran (1915) compares stations in a number of different localities and refers (p. 129) to the exceptional abundance of a single species "round Scotland and the Faeroes." The records of diatom occurrence obtained by the Scripps Institution in a period of more than fourteen years give many indications of locality differences, a few of the more striking being as follows: Daily catches at Farallone Light (about thirty miles seaward from San Francisco) over a period of four years, when abundance was good at Southern California stations, never showed more than negligible occurrence of any kind of micro-plankton. In several series of catches taken by ships plying between San Diego and Seattle catches taken near Destruction Island (off the Washington coast) have been notably larger than others while those from a number of other localities represented in each series have always been small or negligible. Similarly the catches near Abreojos Point in Lower California have appeared notably large in series obtained south of San Diego. These and similar differences are even more impressive if one considers the constituent species as well as total abundance, as is necessary in extensive investigations.

For many locality differences it appears to be fairly evident that topography is responsible. Bigelow (1926, p. 391) says "The fertility in diatoms of the waters over Georges Bank is interesting," and "The prevalence of the genus *Guinardia* on the bank, contrasted with its absence or rarity in the deeper waters of the gulf to the north" and "Turning now to the coastwise belt, diatoms continue a more important factor in the phytoplankton of estuarine situations throughout the summer than they are in the open waters of the deeper parts of the gulf at that season." Numerous other writers indicate similar observations and views, some of them emphasizing the influence of upwelling or

other turbulence caused by bottom or shore line topography of a particular region.

For other locality differences it appears to be assumed by some writers that differences in latitude are mainly influential. Harvey (1928, p. 178) gives certain really good reasons why high latitudes may be more fertile. Johnstone (1908, pp. 202–205) expresses the positive opinion that "the productivity of the sea" is greatest in arctic or sub-arctic regions and he mentions or quotes a number of corroborative statements of various observers and authorities. He says: "Thus the colder seas are richer in life than the warmer ones; or at the very least the amount of life in polar seas is not less than in the tropics." He quotes Kjellman: "One stands as before an insoluble problem when he makes a haul with a tow-net in the Arctic and obtains abundant and strong vegetation, and this at a time when the sea is covered with ice, the temperature is extremely low, and nocturnal gloom predominates even at noon." Comments even more emphatic have been made concerning the diatom production of Antarctic seas. While not antagonistic to such statements and ideas the Scripps Institution of Oceanography long ago suggested the desirability of testing their degree of accuracy: first, because such sweeping generalizations do not seem justified in the absence of concurrent comprehensive surveys of actual production in both low and high latitudes, through at least one annual cycle (preferably several); second, because the reports from high latitudes appear to deal entirely with conditions at the surface level; third, because the most extreme statements concerning excessive abundance of plankton in high latitudes appear to be based on incidental notice rather than on substantial series of careful observations. Avoiding voluminous arguments and citations, perhaps it is permissible to pass this point with the statements that records of the Institution covering sub-tropical latitudes over a period of years show a considerable productivity in some localities, not only at the surface, but to depths as great as sixty meters below the surface (fig. 2), and others covering sub-arctic latitudes which show many localities lacking high productivity at a time when neighboring localities were prolific. With such evidence in hand it seems that generalizations concerning the relative productivity of low and high latitudes are not tenable on the basis of data yet available. (*Cf.* W. E. Allen, 1923, 1925, 1927a, 1929). So far as species composing the populations of plankton diatoms are concerned, many are to be found at times from Panama to Alaska but the genus *Thalassiosira* is much more conspicuous in the higher latitudes.

The evidence obtained by the Scripps Institution as well as that of most literature on plankton supports the view that the high sea is not strongly productive of plankton. Along the Southern California coast the greatest productivity is surely within fifty miles of shore. In other seas, more shallow water or shoals may present influences resembling or helping to conserve those of proximity to exposed land in such a way as to greatly extend the productive area in relation to visible land. Gran (1915, p. 133) has long supported the hypothesis "that the great amount of plankton which occurs in the coastal waters and from thence can spread far out to sea, is first of all due to a permanent supply of nutritive substance from land" and this seems to be in substantial agreement with the views of most other investigators, including those of Southern California. While not supported by enough specific data to be incontestable there is reason for thinking that "flood years" in the San Diego region are especially favorable for production of plankton in spite of the

serious interference to runoff due to impounding of the waters. But even a "flood year" in a semiarid region does not yield enough land materials to carry influence very far to sea and it is probable that the land influence in Southern California more often favors greater productivity near shore by causing "upwelling" in its vicinity (Michael, 1921; *cf.* Harvey, 1928, p. 168).

SOLAR RADIATION

There seems to be general acceptance of, and no objection to, the idea that solar radiation influences life in the sea no less than it affects that on the land. Russell (1927) says "Light is absolutely necessary for the life of all the floating plants" and "That light is an important factor in the behavior of animals is well known." Nevertheless, the details of operation of radiation influences, the phenomena of their transmission and delivery to each organism in the sea, and the identifications of their results in particular cases are still obscure. This is especially true of the phytoplankton, in which the immediate or measureable responses to influence are less easily traced than is the case in some researches on plankton animals. Marshall and Orr (1927) say: "Although sunlight is necessary for photosynthesis, too much of it is injurious. It has been found that diatom cultures grow best away from direct sunlight. . . . Even in the sea, it is possible that in summer the actual surface layer is not the optimum position for diatoms." Figures 1, 2, and 3 appear to support this supposition for the Southern California region, at least in mid-summer, but Moberg's (1928) study of chemical influences affecting the catches represented in these graphs shows that other conditions also favored greatest abundance at several meters below the surface.

RELATION OF DIATOMS TO ANIMALS

In preceding pages of this paper a number of authoritative statements have been quoted to show the importance of diatoms as one of the links in the food chains of the sea. Some of the best direct evidence available was obtained at the Scripps Institution by Esterly (1916, p. 182) who found that "An examination of the digestive tracts of several species of marine copepods shows that diatoms are the organisms whose remains appear most often." However, Esterly himself notes (on the same page) that the food of copepods probably consists largely of organisms lacking shells or other means of leaving recognizable remains. Still the general emphasis on the food values of diatoms is so great that there is risk of forgetting the possibility of other relationships. In particular, it is possible that certain kinds of diatoms may be poisonous to animals (or to certain animals) just as certain land plants are known to be so, and it is possible than when present in great abundance they may interfere more or less with respiration of some animals by clogging the gills. Direct evidence in support of these possibilities is not available in Southern California except that commercial fishermen say that fishing is not good where diatoms are so abundant as to discolor the water. Bullen (1908, p. 291) examined a sample of "stinking water" from the English Channel such as fishermen said indicated absence of fish (mackerel) and found a preponderance of phytoplankton over zooplankton. And since it is known that certain kinds of dinoflagellates (other phytoplankton often occurring with diatoms) sometimes cause great destruction of inshore forms of animal life (Torrey, 1902) it is reasonable to suppose that diatoms may become deterrent or deleterious to animal life under certain circumstances.

CLOUD THEORY OF PHYTOPLANKTON OCCURRENCE

In general discussion of occurrence and distribution of plankton in terms of abundance one is driven by necessity to the use of statements and modes of expression much more definite than are justified by the facts, either known or surmised. Thus arises the apparent absurdity of speaking of the productivity of thousands of square miles of Southern California seas in a given day, week, month, or year when the only evidence available is that obtained from a few pints or gallons of water at a single convenient point. However, this absurdity is more apparent than real so far as characterization of the region as a whole is concerned, the error in exact representation of conditions at any other one point, as compared with the observation point, being partly offset by the *approximation of representation* of the observation point when compared with *all* points belonging to the area. A meteorological observer succeeds in giving us a fairly good working idea of conditions in his region in spite of a wide range of differences at different points in the ocean of air (the atmosphere) when he reports "cloudy" or "partly cloudy" at his station. There is good reason for thinking that an oceanographical observer may succeed in giving a similarly useful general idea of conditions in his region of the ocean of water by reporting the differences in abundance of plankton occurring at his station, although the range of differences may be very wide at different points belonging to the area.

Not only is there this general analogy of practical usefulness of characterization of regional conditions from narrowly localized observations in the two kinds of oceans, but there is also a considerable resemblance in the formation of clouds of different substances in the two kinds of media. While we most often refer to clouds of water vapor when we speak of clouds in air, we also frequently speak of other clouds such as "clouds of smoke," "clouds of gnats," "clouds of dust" and the like. It is, therefore, quite natural to speak of clouds in water and in the ocean. And, in the case of phytoplankton, the usage is commendable because the term cloud leads us to think of plankton occurrences as being similar in appearance to those of water vapor in air which are so familiar to us. In our actual experience we sometimes see rather dense aggregations of plankton in a small area which look in shape and density very much like some of the little clouds of water vapor we see sometimes in the air. When the sea is discolored for miles as described by Moseley and by Haeckel as quoted in the early part of this paper the condition is comparable to that of an "overcast sky." More frequently there are intergradations between these extremes, or perhaps most frequently the resemblance is to those thin clouds scattered about the sky as wisps, and flowing banners, and weird, translucent canopies of fantastic form with highly irregular space relationships. This is particularly true of the minute plants such as diatoms and photosynthetic dinoflagellates which constitute much of the more strictly primary part of the food supply of the sea. Both from boats and from the ends of piers one may see at certain times slight streaks, smears, or tinges of discoloration of the surface of the sea which have form and extent similar to that of many of the thin clouds of vapor in the sky above them. At any rate, there can be no doubt that the idea of plankton clouds has a distinct value as a counterbalance to the idea which might otherwise be allowed to grow in our minds that oc-

currence and distribution of plankton in the sea is uniform or regular in detail in relation to either space or time.

CONCLUSION

In concluding a cursory survey of a field so extensive as this, it is surely appropriate to make a few remarks concerning the general food relationships of the ocean in which photosynthetic organisms assume a conspicuous position. In case of simple death of a diatom (or other phytoplankton) cell, it may be supposed that decomposition by bacteria or other saprophytic forms brings derivatives from the body substance to a soluble or suspended condition in the surrounding water, from which some of them may be removed by another diatom cell for its own use. For some particular atom it may be possible for the circuit to be very short, i.e. diatom—bacterium—sea water—diatom. In most cases it is longer as: diatom—copepod—herring—cod—bacterium—sea water—diatom. (Harvey, 1928, p. 168, gives an excellent diagram illustrating the general possibilities.) Long or short, there is no room for doubt that photosynthetic organisms occupy the key position in the general circuit of food exchanges in the ocean, and that they must be reckoned with sooner or later, even though one may choose, like Brooks, to include animal microplankton under the convenient term of "primary food supply."

LIST OF LITERATURE

Allen, E. J. 1908. Mackerel and sunshine. *Jour. Marine Biol. Assn. United Kingdom*, 8: 394–406. *Plymouth.*

———. 1919. A contribution to the quantitative study of the plankton. *Ibid.*, n.s., 12: 1–8.

Allen, W. E. 1921. Some work on marine phytoplankton in 1919. *Trans. Amer. Micr. Soc.*, 40: 177–181.

———. 1922. Observations on surface distribution of marine diatoms between San Diego and Seattle. *Ecology*, 3: 140–145.

———. 1922a. Quantitative studies on inshore marine diatoms and dinoflagellates of Southern California in 1920. *Univ. Calif. Publ. Zool.*, 22: 369–375.

———. 1923. Observations on surface distribution of marine diatoms of Lower California in 1921. *Proc. Calif. Acad. Sciences*, 12: 437–442.

———. 1925. Statistical studies of surface catches of marine diatoms and dinoflagellates made by the yacht "Ohio" in tropical waters in 124. *Trans. Amer. Micr. Soc.*, 44: 25–30.

———. 1926. Remarks on surface distribution of marine plankton diatoms in the East Pacific. *Science*, 63: 96–97.

———. 1927. Quantitative studies on inshore marine diatoms and dinoflagellates of Southern California in 1921. *Bull. Scripps Inst. Oc.*, Tech. Ser., 1: 19–29. (1922, *ibid.*, 1: 31–38.)

———. 1927a. Surface catches of marine diatoms and dinoflagellates made by U. S. S. "Pioneer" in Alaskan waters in 1923. *Ibid.*, 1: 39–48.

Allen, W. E. 1928. Catches of marine diatoms and dinoflagellates taken by boat in Southern California waters in 1926. *Ibid.*, 1: 201–246.

———. 1928a. Review of five years of studies on phytoplankton at Southern California piers, 1920–1924 inclusive. *Ibid.*, 1: 357–401.

———. 1929. Surface catches of marine diatoms and dinoflagellates made by U. S. S. "Pioneer" in Alaskan waters in 1924. *Ibid.*, 2: 139–153.

———. 1929a. Ten years of statistical studies of marine phytoplankton at the Scripps Institution of Oceanography. *Science*, 70: 416–419.

Bigelow, H. B. 1926. Plankton of the offshore waters of the Gulf of Maine. *Bull. U. S. Bur. Fisheries*, 40: part 2.

Brooks, W. K. 1893. The Genus Salpa. Memoirs from the Biological Laboratory of the Johns Hopkins University, II. Johns Hopkins Univ. Press, *Baltimore.*

———. 1894. The origin of the food of marine animals. *Bull. U. S. Fish Com.* (for 1893), 13: 87–92.

Bullen, G. E. 1908. Plankton studies in relation to the Western Mackerel Fishery. *Jour. Marine Biol. Assn. United Kingdom*, n.s., 8: 269–303.

Cleve, P. T. 1901. The seasonal distribution of plankton organisms. *Kgl. Vet. och Vitt. Samh. Handl.*, XVII. *Göteborg.*

Esterly, C. O. 1916. The feeding habits and food of pelagic copepods and the question of nutrition by organic substances in solution in the water. *Univ. Calif. Publ. Zool.*, 16: 171–184.

EYDOUX et SOULEYET. 1852. Voyage autour du monde sur la corvette "La Bonite." *Zoologie*, v. 2. *Paris.*

FISH, C. J. 1925. Seasonal distribution of the plankton of the Woods Hole region. *Bull. U. S. Bureau Fisheries*, 41: 91–179.

GALTSOFF, P. S. 1932. The life in the ocean from a biochemical point of view. *Jour. Wash. Acad. Sc.*, 22: 246–257.

GOSSE, P. H. 1846. The Ocean. *London.*

GRAN, H. H. 1912. Pelagic plant life. Chapter VI, The Depths of the Ocean, by Murray and Hjort, *London.*

———. 1915. The plankton production of the North European waters in the spring of 1912. Bull. Planktonique, 1912. Conseil Permanent International pour l'Exploration de la Mer, *Copenhagen.*

———. 1930. The spring growth of the plankton at Møre in 1928–29 and at Lofoten in 1929 in relation to its limiting factors. *Skrifter utgitt av det Norske Videnskaps-Akademi i Oslo.* No. 5. *Oslo.*

HAECKEL, E. 1890. Planktonstudien. *Jena.* (English translation in *Rept. U. S. Fish Com.*, 1893) (for 1889–91).

HARVEY, H. W. 1928. Biological Chemistry and Physics of Sea Water. *New York.*

HENSEN, V. 1887. Ueber die Bestimmung des Planktons oder des im Meere treibenden Materials an Pflanzen und Thieren. Fünften Bericht der Kommission zur wissenschaftlichen Untersuchung der deutschen Meere, in Kiel, 1882–1886 (1887), Vols. XII–XVI, pp. 1–107, Taf. I–VI, tables. *Berlin.*

HERDMAN, W. A. 1908. Twenty-first annual report of the Liverpool Marine Biological Committee and their biological station at Port Erin. *Proceedings and Transactions, Liverpool Biological Society*, 22: 94–197.

———. 1922. Some results of plankton investigation in the Irish Sea. Spolia Runiana. V. (Extracted from *Jour. Linnean Soc. Botany*, 46: 141–170.)

———. 1923. Founders of Oceanography. *London.*

HJORT, JOHAN. 1912. Pelagic animal life. Chapter IX, The Depths of the Ocean, by Murray and Hjort. *London.*

HORNELL, J., and NAYUDU, M. R. 1924. A contribution to the life history of the Indian sardine with notes on the plankton of the Malabar Coast. *Madras Fisheries Bulletin*, 17: 129–197. *Madras.*

HUSTEDT, F. 1930. Die Kieselalgen. In Rabenhorst's Kryptogamen-Flora von Deutschland, Osterreich und der Schweiz, Band VII. *Leipzig.*

HUXLEY, T. H. 1902. The Scientific Memoirs of Thomas Henry Huxley, v. 4. *London.*

JOHNSTONE, JAMES. 1908. Conditions of Life in the Sea. Cambridge Biological Series. *Cambridge.*

KARSTEN, G. 1928. Bacillariophyta (Diatomeae) in Engler and Prantl, Die natürlichen Pflanzenfamilien. Zweite Auflage. II.

LEBOUR, M. V. 1921. The food of young clupeoids. *Jour. Marine Biol. Assn. United Kingdom*, 12: 458–467. *Plymouth.*

———. 1922. The food of plankton organisms. *Ibid.*, 12: 644–677.

———. 1923. The food of plankton organisms. II. *Ibid.*, 13: 70–92.

———. 1930. The Planktonic Diatoms of Northern Seas. *London.*

LOHMANN, H. 1911. Über das Nannoplankton und die Zentrifugierung kleinster Wasserproben zur Gewinnung desselben im lebenden Zustande. *Internationale Revue der Gesamten Hydrobiologie*, etc., 4: 1–38.

———. 1912. Die Probleme der modernen Planktonforschung. Verhandlungen der Deutschen Zoologischen Gesellschaft auf der zweiundzwanzigsten Jahresversammlung zu Halle.

MANN, A. 1930. The artistry of diatoms. *Carnegie Inst. of Wash. News Service Bull.*, School Ed., 2: 11–15.

MARSHALL, S. M., and ORR, A. P. 1927. The relation of the plankton to some chemical and physical factors in the Clyde Sea area. *Jour. Marine Biol. Assn.*, 14: 837–868.

MICHAEL, E. L. 1921. Effect of upwelling water upon the organic fertility of the sea in the region of Southern California. *Special Publ. Bernice P. Bishop Museum* No. 7, pp. 555–595. *Honolulu.*

MOBERG, E. G. 1918. The interrelation between diatoms, their chemical environment, and upwelling water in the sea, off the coast of Southern California. *Proc. Nat'l. Acad. Sc.*, 14: 511–518.

MOSELEY, H. N. 1879. Notes by a Naturalist on the "Challenger." *London.*

———. 1882. Pelagic life. *Nature*, 26: 559–564.

NATHANSOHN, A. 1906. Über die Bedeutung vertikaler Wasserbewegungen für die Produktion des Planktons im Meere. *Abhandlungen der Mathematisch-Physischen Klasse der Königlich Sächsischen Gesellschaften*, 29: 355–441. *Leipzig.*

OSTENFELD, C. H. 1903. Phytoplankton from the sea around the Faroes. Botany of the Faroes, II. *Copenhagen.*

OSTWALD, W. 1903. Über eine neue theoretische Betrachtungsweise in der Planktologie, insbesondere über die Bedeutung des Begriffs der "inneren Reibung des Wassers" für dieselbe. *Forschungsberichte aus der Biologischen Station zu Plön*, Teil X, pp. 1–49. *Stuttgart.*

PECK, JAMES I. 1894. On the food of the menhaden. *Bull. U. S. Fish Com.* (for 1893), 13: 113–116.

PECK, J. I., and HARRINGTON, N. R. 1898. Observations on the plankton of Puget Sound. *Trans. N. Y. Acad. Sc.*, 16: 378–387.

PELLETAN, J. 1891. Les Diatomées. *Paris.*

PHIFER, L. D. 1933. Seasonal distribution and occurrence of planktonic diatoms at Friday Harbor, Washington. *Univ. of Washington Publ. in Oceanography*, 1: 39–81.

RAFTER, G. W. 1900. The Microscopic Examination of Potable Water. *New York.*

RUSSELL, F. S. 1927. The vertical distribution of plankton in the sea. *Biological Reviews*, 2: 213–262. *Cambridge.*

RYDER, J. A. 1882. The protozoa and protophytes considered as the primary or indirect source of the food of fishes. *Bull. U. S. Fish Com.* (for 1881), 1: 236–251.

SCHÜTT, F. 1896. Bacillariales. Engler und Prantl: Die natürliche Pflanzenfamilien, I. Teil, Abt. 1b. *Leipzig.*

SLEGGS, G. F. 1927. Marine phytoplankton in the region of La Jolla, California during the summer of 1924. *Bull. Scripps Inst. Oc.*, Tech. Ser., 1: 93–117.

TAYLOR, F. B. 1929. Notes on Diatoms. *Bournemouth.*

THOMPSON, C. WYVILLE. 1877. The voyage of the 'Challenger.' *The Atlantic*, v. 1. *London.*

TORREY, H. B. 1902. An unusual occurrence of dinoflagellates on the California coast. *American Naturalist*, 36: 187–192.

WEST, G. S. 1916. Algae. 1. (including Bacillariales). *Cambridge.*

WHIPPLE, G. C. 1914. The Microscopy of Drinking Water. *New York.*

THE NERVOUS SYSTEM OF THE EARTHWORM

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THE nervous system of the earthworm has doubtless received the attention of more morphologists and physiologists than has that of any other invertebrate. Since it is still frequently used in investigation, it is of importance to ascertain the present state of knowledge concerning its structure and function and the manner in which this knowledge has been accumulated. The literature dealing with the nervous system of earthworms (Lumbricidae and allies) has been treated in several monographs, among which the most recent is by Stephenson (121). The present account aims to show how the nervous system of the adult earthworm has been used as material in the study of invertebrate neurology in general.

HISTORICAL DEVELOPMENT

Very few papers dealing with invertebrate nervous systems appeared before 1800. The first accounts were brief descriptions of the principal gross components, culminating in those by such naturalists as Cuvier. Then followed a period of interest in comparative morphology during which the parts of the nervous system in different animals were compared. During this same period (approximately from 1825 to 1850) a few microscopists applied their methods to nerves in different organisms and distinguished between globules and tubes (nerve cell bodies and fibers). Near the middle of the century the interest in comparative morphology led to phylogenetic studies aiming to show relationships among and within groups on the basis of similarities in structure. About 1870 interest in special histology came to the front, and an attempt was made to describe the details of different components of the nervous system, and from this knowledge to reason concerning their function. Fixed and stained tissues came to be used more generally, and three problems were uppermost: the origin and nature of nerve "tubes," the nature of the connections between them in the central nervous system, and the structure of the nerve cells. Since 1890 increasing emphasis has been upon the function of the nervous system. This has led to experimental work such as the study of motor coördination in intact and operated specimens and the use of drugs and of electrical methods. Some of the inferences concerning function that were drawn from the structure of the nerve elements have been substantiated while others have been disproved.

The development of interest in the nervous system of the earthworm closely paralleled this general development of invertebrate neurology. The occurrence of papers dealing primarily with gross morphology, histology, and physiology of the nervous system of the earthworm in different countries is indicated in table 1. This table shows that the first histological study appeared nearly forty years after the first account of gross morphology of the nervous system and that the first physiological paper appeared approximately thirty years after the first histological one.

It shows that each subject has been studied in cycles. For example, peaks of interest in the histology of the nervous system appeared during 1861–1865, 1891–

1895, 1906–1915, and 1926–1930. The peak in 1891–1895 is definitely correlated with the application of methylene blue and Golgi methods to invertebrate material, the others with more general interests of the periods. The recent high peak in this field indicates that the next decade will not be particularly productive of papers dealing with the histology of the nervous system of the earthworm. Similarly, papers dealing with the physiology of the nervous system of the earthworm reached peaks in 1901–1905, 1921–1925, and the indication is that another will be reached during the next few years.

This table also shows that most of the gross morphological studies were done in France and England, that in the histological investigations Germany leads, while second place is nearly equally shared by France and the United States. Further, Germany and the United States have nearly equally contributed to the physiological papers, with almost none from other countries. In each subject the shift has been toward the United States in recent years.

TABLE 1

Occurrence of Papers Dealing with the Gross Morphology, Histology, and Physiology of the Nervous System of the Earthworm from 1816 to 1933. Papers Dealing with Regeneration Are not Included. Countries are Those in Which Work was Done; Some Papers from Other Countries Are not Included

YEARS	GROSS MORPHOLOGY						HISTOLOGY						PHYSIOLOGY					
	France	Germany	England	U. S. A.	Japan	Total	France	Germany	England	U. S. A.	Japan	Total	France	Germany	England	U. S. A.	Japan	Total
1816–'20	1	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—
1821–'25	—	2	1	—	—	3	—	—	—	—	—	—	—	—	—	—	—	—
1826–'30	1	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—
1831–'35	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
1836–'40	—	—	1	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—
1841–'45	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
1846–'50	2	—	—	—	—	2	—	—	—	—	—	—	—	—	—	—	—	—
1851–'55	1	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—
1856–'60	—	—	1	—	—	1	1	—	—	—	—	1	—	—	—	—	—	—
1861–'65	1	—	2	—	—	3	—	3	1	—	—	4	—	—	—	—	—	—
1866–'70	—	—	—	—	—	—	1	—	—	—	—	1	—	—	—	—	—	—
1871–'75	2	—	—	—	—	2	—	—	—	—	—	—	—	—	—	—	—	—
1876–'80	—	—	—	—	—	—	1	1	—	—	—	2	—	—	—	—	—	—
1881–'85	1	—	—	—	—	1	1	1	—	—	—	2	—	1	—	—	—	1
1886–'90	—	—	1	—	—	1	2	3	—	—	—	5	—	2	—	—	—	2
1891–'95	—	1	1	—	—	2	1	6	—	2	—	9	—	2	—	—	—	2
1896–'00	—	—	—	1	—	1	1	3	—	—	—	4	—	3	—	—	—	3
1901–'05	—	—	—	—	—	—	—	3	—	—	—	3	—	3	—	1	—	4
1906–'10	—	—	—	—	—	—	5	2	—	—	—	7	—	—	—	1	—	1
1911–'15	—	—	—	—	—	—	2	6	—	—	—	8	—	—	—	3	—	3
1916–'20	—	—	—	—	—	—	1	1	—	1	—	3	—	1	—	4	—	5
1921–'25	—	—	—	1	—	1	—	—	—	4	—	4	1	2	—	5	1	9
1926–'30	—	—	—	1	1	2	—	—	1	5	4	10	—	1	—	3	—	4
1931–'33	—	—	—	—	—	—	—	—	—	—	—	—	—	2	1	3	—	6
Total.....	9	3	7	3	1	23	16	29	2	12	4	63	1	17	1	20	1	40

GROSS MORPHOLOGY OF THE NERVOUS SYSTEM OF THE EARTHWORM

In 1672 Willis (135) recognized a white lobe above the oesophagus of the earthworm as the brain, "cerebrum mole perexiguum." Cuvier (26) was one of the first to identify the divisions of the nervous system of the earthworm. He observed the ventral nerve cord, two pharyngeal commissures and the dorsal brain or suprapharyngeal ganglion. Referring to *Lumbricus* he said, "Le cordon nerveux n' est qu'une suite d'une infinité de petits ganglions serrés les uns contre les autres."

Leo (78) and Roth (111) also identified these parts, and Home (57), Morren (88) and Anderson (1) added more details. Home figured two anterior nerves arising from the brain of the earthworm, one from each pharyngeal commissure, one pair from the subpharyngeal ganglion, and two or three pairs from each remaining ganglion. Anderson stated that two pairs of nerves emerge from each ventral ganglion and two pairs from the cephalic ganglion or brain. He considered the second and third segmental nerves to constitute one single root. Thus by 1840 the gross components of the nervous system of the earthworm had been identified.

In 1848 Blanchard (8) advanced the idea that each class of invertebrates has its own basic pattern of nervous system and that the arrangement of ganglia can be used as a basis of classification. He supported this contention by a study of a variety of groups including earthworms. In using this new method of classification Quatrefages (103) maintained that the number of segments in earthworms and leeches is determined by the number of ganglia rather than by the external segmentation. Perrier (96, 97, and 98), Benham (5), and Beddard (4) also made comparative studies of the nervous system of different species of earthworms. They used the position of the brain, the number of cerebral nerves, the degree of separation of the ventral ganglia, and other variations in the central nervous system as a basis of classification, and showed that there are appreciable differences in the nervous systems of different species.

Clarke (23) made the first really detailed study of the ganglia of *Lumbricus*. He described the brain as a bilobed mass giving rise to the pharyngeal crura or commissures and to two cephalic nerves which branch to the upper and lower prostomium. In the brain he distinguished an outer cellular lamina and an inner fibrous mass, a fan-like spreading of the roots of the prostomial nerves and a transverse band of fibers between the two lobes. He homologized the dorsal part of the cephalic ganglion with the lower part of the ventral chain because of the similar distribution of cells in each, and drew an analogy between the transverse commissure in the brain and either the corpora quadrigemina or corpus callosum.

In 1865 Udekem (129) published some colorful but inaccurate plates in which he showed nerves leaving the cord and branching symmetrically among the muscles. The distribution of the peripheral nerves was treated more completely, however, by Hesse (54), Fling (31), and Hess (51). Hesse maintained that the first and third nerves in a segment are mainly motor and that the second nerve serves most of the sense organs in the segment. He described the innervation of the anterior end in *Lumbricus herculeus*, and Hess described it in *Lumbricus terrestris*. Hess used both gross dissections and serial sections in tracing the nerves. His general results are presented in figure 1. This figure shows that the pharyngeal commissures innervate the first segment and that the anterior part of the subpharyngeal ganglion inner-

vates the second and third, the posterior part the fourth segment. This indicates that the subpharyngeal ganglion probably represents the fusion of three segmental ganglia. Hess states that the caudal segment has either five or six pairs of nerves and that each pair of segmental nerves forms a complete ring around the body. According to Fling, the branches of these nerve rings overlap on both the dorsal and

In addition to the ganglia and the nerves arising from them, there is in the earthworm a pharyngeal plexus which was first described by Quatrefages (102) and later by Clarke (23). The former said that six branches from each pharyngeal commissure are connected with a nerve plexus over the pharynx; the latter that four or five short branches from each commissure extend to the plexus. In 1865 Lankester

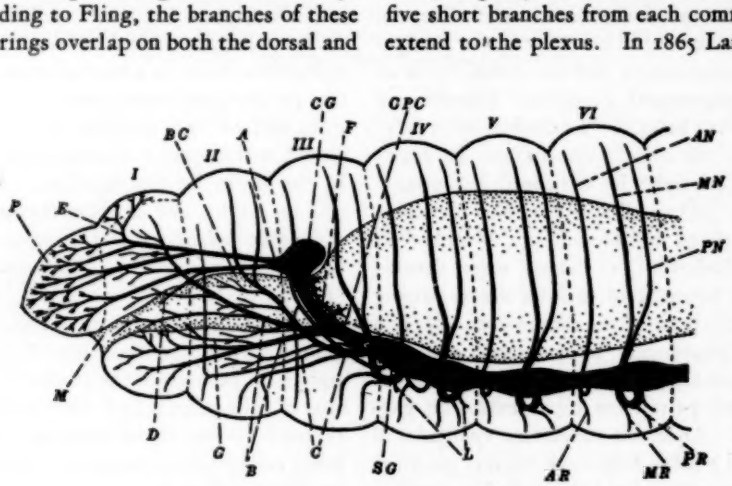

FIG. 1. DRAWING SHOWING A LATERAL VIEW OF THE ARRANGEMENT OF THE LARGER NERVE TRUNKS IN THE LEFT HALF OF THE ANTERIOR SEGMENTS OF THE EARTHWORM, LUMBRICUS TERRESTRIS

A, nerve from lateral region of cerebral ganglion which passes to prostomium; *AN*, dorsal ramus of anterior segmental nerve; *AR*, ventral ramus of anterior segmental nerve; *B*, nerve from near middle region of circumpharyngeal connective which passes to segment 1; *BC*, buccal cavity; *C*, nerves from ventral region of circumpharyngeal connective which pass to segment 2; *CG*, cerebral ganglion; *CPC*, circumpharyngeal connective; *D*, branch of nerve to prostomium that supplies tissues of dorsal region of buccal cavity; *E*, nerve that supplies the portion of the prostomium in the dorsomedian region of segment 1; *F*, gangliated thickening of enteric nerve plexus; *G*, branch of nerve to segment 1 that supplies tissues of ventral region of buccal cavity; *L*, septal nerve; *M*, mouth opening; *MN*, dorsal ramus of median segmental nerve; *MR*, ventral ramus of median segmental nerve; *P*, prostomium; *PN*, dorsal ramus of posterior segmental nerve; *PR*, ventral ramus of posterior segmental nerve; *SG*, subpharyngeal ganglion; *I–VI*, segments 1 to 6.

(This figure was drawn by Dr. W. N. Hess and is reproduced by his permission.)

ventral sides. Fling also stated that the posterior segmental nerves gives branches to the septa and intestine in addition to the musculature.

The nervous system of *Perichaeta megascolidioides* (Imai, 62) is peculiar in that eight to ten cerebral nerves leave the borders of the cerebral ganglion and supply the prostomium, buccal cavity, and part of the first segment.

(75) referred to the pharyngeal plexus as a sort of reflex center which "presides over the operations of the viscera" while the subintestinal cord is locomotor in function. Rorie (110) suggested that the suprapharyngeal ganglion is analogous to the cerebral hemispheres of man, the ventral chain to the sympathetic system and the pharyngeal plexus to the vagus. Chen (21) made careful dissections of the finer branches of

this plexus in *Lumbricus*. He supported Quatrefages by saying that the plexus arises as a chain of nerve cells from six nerves from each pharyngeal commissure from this chain anterior and posterior nerve trunks branch and anastomose freely around the pharynx.

It may be concluded from this discussion that different species of earthworms differ somewhat in the distribution of nerves, but that, in general, each segmental ganglion gives rise to three pairs of lateral nerves, that the brain supplies the prostomium and part of the first segment, that the pharyngeal commissures give rise to a pair of nerves to the first segment and to six pairs of small nerves which join a pharyngeal plexus, and that nerves from the subpharyngeal ganglion innervate the second, third, and fourth segments.

HISTOLOGY OF THE CENTRAL NERVOUS SYSTEM

Most of the early morphologists mentioned in the preceding section observed that the brain and nerve cord of the earthworm consist essentially of a sheath, an outer layer of globules (nerve cells), and an inner mass of tubes (nerve fibers), and that these structures are arranged symmetrically right and left. The study of these details of the nervous system of the earthworm contributed to at least five problems of general interest: the number of processes in neurones, the origin of nerve fibers, the manner of connection between neurones, the paths followed by nerve fibers in the ganglia, and the finer structure of nerve cells. The first two of these may be considered as settled, the others as not yet settled. They can best be understood by a study of the manner of development of each problem.

One of the first problems to attract histologists to earthworms concerned the number of processes in the nerve cells. These cells were first studied in untreated macerations of the nerve cord, then after treatment with various acids, both inorganic and organic. In 1856 Faivre (30) concluded from such preparations, treated and untreated, that there are apolar, unipolar, bipolar and multipolar nerve cells. In 1863 Rorie (110) studied untreated preparations with the aid of a very bright light and reached essentially the same conclusions as Faivre. He added the observation that multipolar cells in the brain give rise to the fibers of the transverse commissure which connects the two lobes of the brain. In the same year Walter (133) treated the nerve cord with acid and observed two lateral groups of unipolar and a central group of multipolar cells. Claparède (22) and Nansen (89 and 90) used a variety of fixatives; they doubted the existence of multipolar cells. The latter maintained that all ganglion cells are really unipolar, the shorter branches being protoplasmic and nutritive.

The problem was ultimately settled by Cajal (18) and Boulé (9 and 10) who used elaborate methods of silver impregnation rather than the less specific fixatives and stains used by the earlier investigators. They demonstrated that the apolar cells in the nerve cord of *Lumbricus* are neuroglia and not true nerve cells, and that most of the nerve cells are unipolar or multipolar; a few are bipolar.

This discussion concerning the number of processes in the ganglion cells led to a study of the origin of the nerve processes. This was studied more intensively in other invertebrates, and the earthworm contributed only incidentally to the solution of the problem. The early histologists agreed that the "Punktsubstanz" of the neuropile is fibrous in nature. Vignal (132), among others, contended that some of these fibers are independent, while others, for example Faivre (30), said that they are connected with nerve cells.

Walter (133) and Nansen (90) said that both views are correct. The enunciation of the neurone theory by Waldeyer in 1891 and the use of methylene blue and the Golgi method of nerve impregnation enabled Retzius (107) to show conclusively that all nerve fibers are connected with nerve cells.

Another controversy ensued concerning the connections between neurones in the central nervous system of the earthworm. Vignal (132) in a general review in 1883 postulated anastomoses of processes in the ventral nerve cord as did Walter (133). Nansen (89 and 90) and Retzius (107), however, opposed this view and maintained that true fusion does not occur between nerve fibers, but that the fibers merely come into close contact with each other. In 1897 Apathy (2) contended, on the basis of methylene blue preparations, that in the nerve cords of the leech and earthworm anastomoses occur between the fibers and among the primitive "fibrils" in the nerve cells. Apathy's conclusions with respect to fusion of fibers were not accepted by Lenhosšék (77), Cajal (18), Boulé (9 and 10), and Schneider (112), who worked with silver methods. No recent investigators have dealt with this question in the earthworm, but the bulk of evidence obtained with other animals as well as the work of the investigators just mentioned favors synaptic contact and not fusion of nerve fibers in the neuropile of the central nervous system.

The study of the manner of connection among the nerve fibers led to a study of the course of neurones in the ganglia of the earthworm. The paths of many neurones were traced by Haller (43 and 44), Cerfontaine (20), Retzius (107), and Krawany (71), each of whom used specific nerve stains. These histologists agreed that in the ganglia commissural cells connect sensory with motor neurones and that they connect either the two sides of the same ganglion or two consecutive ganglia. They said that the connection between two ganglia may be homolateral or crossed, and that more motor processes than sensory processes cross from one side to the other. Fortuyn (33) constructed diagrams of the paths of neurones on the basis of the descriptions by these histologists. These diagrams indicate extreme differences in the views held concerning details of the neurone paths. Figure 2 is a series of similar diagrams in which each type of commissural and motor neurone figured by these histologists is schematically presented. These diagrams show twenty-two types of motor neurone and twenty-three types of strictly commissural neurone. Of all these, the main axones of twenty-three are homolateral, and of twenty-two are contralateral. Not a single type of neurone was figured by all four histologists; three types of neuron were figured by three of them; thirteen types were figured by two. This diversity of opinion may be explained by the fact that some neurones and some axone branches are not made visible by these methods and by the fact that each ganglion of the cord contains approximately 120 to 150 cells (Stephenson, 121) of which only a small portion were mapped by any one investigator.

Ogawa (94 and 95) and Tuge (127) estimated the number of cells and fibers in the ganglia of *Perichaeta* and *Allolobophora* and concluded that in the neuropile there are approximately twice as many fibers as there are cells in each ganglion.

Smallwood (118) recently emphasized the extensive branching of central neurones. He and Rogers (109) drew the conclusion that numerous cells participate in even the simplest reactions and that the two-cell reflex is probably not the dominant pattern.

The structure of the individual nerve

cells has been studied fully as extensively as the nature of connections between cells and with equally divergent results. Faivre (30) asserted that the untreated nerve cells are fluid in content. He pointed out that most of the fibers are non-medullated. Vignal (132), Walter (133), and Horst (59) applied acid fixatives to the nerve cord. Vignal contended that the cells are granular. Walter and Horst said that they are fibrillar. Approximately twenty years after Horst's paper the structure of ganglion cells was studied with the aid of the newer silver and methylene blue methods. These methods were used in investigating nerve cell structure in the earthworm by Pflücke (99), Cajal (18), Boulé (9, 10, and 11), Kowalski (69), and Szüts (125 and 126). They maintained that they observed nets of anastomosing fibrils in the cell bodies. Boulé figured an eccentric nucleus and two fibrillar nets, inner and outer; he said that these nets are continuous with the fibrils in the nerve processes. Schneider (112), using a variety of methods, contended that the motor fibers contain few large fibrils and that the sensory fibers contain many fine ones. Bialowska and Kulikowska (6) described a fibrillar Golgi-Kopsch apparatus among the neurofibrils in the cell bodies of the ventral nerve cord of *Lumbricus*. These observations of anastomosing neurofibrillar nets were made entirely on fixed and stained or impregnated tissues, not on living cells. In the light of recent evidence (Bozler, 15) that anastomoses among fibrils are not seen in living nerve cells and the increasing recognition of artifacts of fixation, a reinvestigation of this question might give important results.

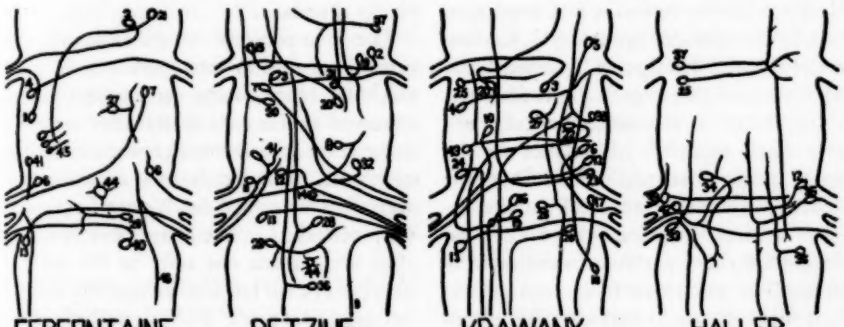

FIG. 2. DIAGRAMS OF TYPES OF MOTOR AND COMMISSURAL NEURONES IN ONE GANGLION OF THE NERVE CORD TO SHOW PATHS OF PRINCIPAL AXONES

Figures condensed from those by Cerfontaine (20), Retzius (107), Krawany (71), and Haller (44). The main axones of neurones 1–4 leave cord by segmental nerve I, neurones 5–8 by nerve II, neurones 9–14 by nerve III, axones of neurones 15–26 pass in anterior or posterior direction, neurones 27–45 are compound in their branches, neurone 46 is sensory. Neurones which were originally shown on both sides of a ganglion are here shown on only one side.

Two other problems, less controversial than the preceding ones, are important in the histology of the central nervous system of the earthworm. These concern the giant fibers and the non-nervous constituents. In the dorsal part of the nerve cord of most earthworms there are three giant nerve fibers. These were first described in 1862 by Leydig (79 and 80). He traced them to the base of the pharyn-

geal commissures and said that they blacken with osmic acid like myelinated vertebrate fibers but unlike other fibers of the earthworm cord. Later (81), he figured an outer clear zone and an inner fibrillar region in these fibers and asserted that they function in the transmission of impulses. Claparède (22) stated that, of the three giant fibers in *Lumbricus*, the median one extends forward farther than the two lateral ones. Horst (59) contended that the giant fibers have a homogeneous fluid content. The giant fibers of the earthworm were studied with the aid of specific nerve stains and impregnations by Friedländer (34 and 36), Cerfontaine (20) and Hönig (58). Friedländer and Hönig said that each giant fiber has its cell body in the posterior ganglion. Cerfontaine agreed with respect to the lateral giants but maintained that the median one arises from a cell in the anterior ventral ganglion. Keyl (66) asserted that there are two branches from the median and three from each lateral giant fiber in each segment; he traced some of these branches to large nerve cells in the ventral part of the cord.

In 1926 Stough (122) made a very intensive study of the giant fibers in *Lumbricus*. He traced connections from the median giants to two pairs and from each lateral giant fiber to one pair of giant cells and to several smaller ones in each segment. Stough stated that each giant fiber consists of compressed axones and that the diameter of each giant fiber is not constant throughout its length. He found two ventral giant fibers in addition to three dorsal ones and maintained that in each segment there is in the giant fibers on oblique partition continuous with their myelin, on the two sides of which the fibers stain differently. He suggested that these septa might constitute a sort of synapse. Smallwood and Holmes (119) confirmed Stough's conclusions concerning the ventral giant fibers and traced fibrils out to the neuropile, from one lateral giant fiber to another, and from each giant fiber to cells in each segment in *Lumbricus* and *Eisenia*. The preceding evidence indicates that the earlier investigators found only the cells in the posterior and anterior ganglia connected with the giant fibers, whereas these fibers actually give off branches to cells in each ganglion. This evidence also indicates that the connections of the giant fibers both with the neuropile and with each other are relatively abundant.

The non-nervous constituents of the central nervous system remain to be considered. Many of the early investigators observed apolar cells which they assumed to be nerve cells but which were in reality neuroglia. Glial cells in the earthworm were first described by Walter (133) and Claparède (22). The latter observed that they are present not only in the central nervous system but also around the lateral nerves. Claparède also described three sheaths of the cord, an outer neurilemma, a median muscular layer, and an inner neurilemma. Joseph (64 and 65) described the neuroglia in several groups of invertebrates and maintained that they are fibrous in structure. Cajal (18), Schneider (112), Boulé (11), Comes (24), and Havet (47) extended and supported these studies of the sheath and neuroglia. Havet, by means of a gold chloride technique, observed that the neuroglia may be either fibrous or granular and that they are intimately connected with both nerves and blood-vessels. Stough (122) and Holmes (56) described supporting tissue between and around the giant fibers. Holmes maintained that the sheath of the lateral nerves differs from that of the ganglia only in its lack of muscle cells.

The above account indicates that the

earthworm contributed to the general conclusions that central nerve cells may be unipolar, bipolar, or multipolar, and that all fibers originate in cell bodies. It also indicates that, although much knowledge is available concerning the neurone paths, the fibrillar structure of nerve cells, the nature of the giant fibers and of the neuroglia and sheath of the central nervous system of the earthworm, many histological problems remain unsettled. For example, the function of different types of neurone as indicated by the course of the processes of these cells is largely unknown. The nature of the fibrillar network in the cells and its relation to the fibrils of the axones remain undetermined, as does the nature of the contact between fibers in the neuropile and in the giant fiber tracts. The relation between the small axones of the giant fibers and the giant cells and the branches between the fibers remains to be settled.

PERIPHERAL COMPONENTS OF THE NERVOUS SYSTEM

In addition to these central elements, two peripheral components of the nervous system, the peripheral network or plexus, and the sensory cells, may be considered. Retzius (107), Smirnow (120), and Langdon (73) maintained that there is a network of nerve fibers beneath the epithelium. Smirnow added that the blood vessels also are covered by such a network. Kolmer (68) figured fibrils passing from the epithelial sensory cells of *Lumbricus* into the subepithelial plexus. Dechant (28) confirmed these findings, stated that nerve cells as well as fibers are present in the plexus, and that a similar subepithelial plexus exists in the pharynx. Hess (51 and 52) showed that the network occupies an intermediate position between the sensory cells and the central nervous system and found continuity between subepidermal and intermuscular plexi. Smallwood (115, 116, and 117) found a nerve network in these regions and also on the blood vessels, septa, nephridia, and digestive tract. He contended that the sensory nerves do not contain so many fibers as there are sensory cells; hence convergence of fibers from the sensory cells must occur in the subepithelial plexus.

Dechant, Hess, and Smallwood used a variety of methods and maintained that the peripheral plexus is a true net of anastomosing fibers. Langdon found no such continuity. The other histologists were largely non-committal on this point. The question of whether the peripheral plexus is a true net remains unsettled. In fact, the existence of any true peripheral net is debatable. As opposed to a network, Bozler (15) found discontinuous synapses in coelenterates. Numerous neuro-histologists have cast doubt upon the validity of the silver methods for distinguishing contact from continuity of fibers. Physiological evidence will be presented below against the existence of a true net in the earthworm.

Knob-like nerve endings among the muscles were described by Retzius (107), and branching nerve endings by Smallwood (117). It is likely that these are motor endings.

Dawson (27) found nerve cells in *Lumbricus* among the muscles and on the nerve rings, particularly where the segmental nerves branch. He asserted that these cells may be sensory in nature, probably proprioceptive. The same sort of nerve cell among the muscles and between the epidermis and muscles was described later in *Pheretima* and *Eisenia* by Zyeng (138).

Epithelial cells, supposed to be sensory in nature, are considered by numerous investigators. Mojsisovics (84), Horst

(60), Ude (128), Vejdovsky (131), Cerfontaine (19), and Lenhossék (77) described epidermal cells which bear hairs at their peripheral ends and are frequently found in small groups about a pore canal. They are connected centrally to fibers which pass to the central nervous system and are undoubtedly sensory.

In 1895 Langdon (73 and 74) maintained that thirty or more of these sensory cells, each with a terminal hair, constitute a sense organ and that each cell gives rise to a nerve fiber proximally. She found an anterior, median, and posterior zone of these sense organs in each segment and contended that they are most numerous in the anterior, less numerous in the posterior, and least in the middle regions of the body. Havet (46) described the sensory cells in the epidermis of the earthworm as pyramidal, pyriform, fusiform, or moniliform.

Smirnow (120), Retzius (108), and Langdon (73) found free endings of sensory nerve fibers among the epidermal cells.

Hesse (54 and 55) found these sense organs in the epidermis and also other sensory cells of a more specialized sort in the epidermis, in peripheral ganglionic masses in the prostomium and first segment, and sometimes near the surface of the brain. These cells, he said, have a clear cytoplasm and a large well-differentiated body which he called a "Binnenkörper." Their shape, distribution, and abundance vary among different species. He found these particular cells to be most abundant in the regions which are most sensitive to light, and called them "Lichtzellen" or photoreceptors. Kowalsky (70) and Hess (53) further described the "Lichtzellen" of Hesse. Hess found in 1925, by means of silver impregnations that the "Binnenkörper" and the rest of the cytoplasm contained numerous anastomosing neurofibrils and that part of the former body focuses light on the fibrillar net. It is assumed that all of the other epithelial cells and organs are sensitive to tactile or chemical stimulation, but no definite information concerning their sensitivity is available, hence strict proof that these cells are sensory in nature is lacking.

REGENERATION

Earthworms have frequently been used in the study of regeneration of nervous tissue. Early observers, Bonnet, Spallanzani, and others, reported instances of regeneration of lost parts, but this was denied in the earthworm by Williams (134) as late as 1851. Newport (91) in 1855 exhibited three worms in which more than a third of the posterior part of the body had regenerated.

Heschler (49) stated that, when a number of segments are removed, cells are pushed out from the old nerve cord and that the brain can be regenerated from epithelial cells. Rand (105, 106) claimed that both the brain and the ventral nerve cord of a regenerating region come chiefly from epithelium, but that undifferentiated cells in the ganglia may become nerve cells. Hall (42) maintained that ventral nerve cells may migrate into a cut region of the nerve cord. Nuzum and Rand (93) stated that even new pharyngeal epithelium can contribute to a regenerating brain. Schwartz (113), using the Nissl technique, claimed to find that connective tissue is transformed into nerve cells. Thus three tissues have been stated to give rise to regenerating nerve cells. It is difficult to believe that connective tissue of mesodermal origin can contribute to nerve cells. In fact, the problem is far from settled.

Morgan (86), Hunt (61), Siegmond (114), and Bailey (3) said that the presence

of a free cut end of the ventral nerve cord is necessary for regeneration. Goldfarb (40) maintained that it is not necessary. Bailey (3) asserted that if the free end of the nerve cord is folded back on the cord leaving several segments without any connection with the central nervous system after part of the body is removed, usually no nervous tissue and sometimes no new head or tail is regenerated. Kropp (72) recently found that when a brain from another worm is transferred to the dorsal region of a regenerating anterior end, the brain is resorbed, but when transplanted to the ventral region, it is incorporated into the new subpharyngeal ganglion. The cut end of the nerve cord, therefore, appears to be a center of regeneration.

THE FUNCTION OF THE NERVOUS SYSTEM

One of the most interesting problems in the physiology of the nervous system of the earthworm concerns the functions of the central nervous system and the peripheral plexus in conduction of impulses in locomotion. Physiological studies have also contributed to the problems of the nature of locomotor peristalsis, segmental independence, the function of giant fibers, and cephalic dominance.

Fundamental work was done on the first of these problems by Friedländer (35 and 37) who removed the ventral nerve cord from several segments of an earthworm. He observed a flaccid condition in the muscles of these segments and stated that when a locomotor peristaltic wave passes backward, there is no contraction in the denervated segments except as they are pulled out by the contracting anterior ones. He said that this region pulls like a loose string on the segments behind it, and that these segments then begin active contraction apparently coördinated with the anterior region. He then tied the two halves of a transected earthworm together with a thread and observed similar coördination between them. He also observed that tactile stimulation of the posterior segments initiated a forward moving wave which stopped at the segments lacking the nerve cord. He concluded that the mechanical effect of the pull of one region upon another and traction upon the substratum initiate peristalsis. He postulated a reciprocal reflex of "thickening" and "thinning" which involves alternate contraction and relaxation of the two sets of muscles and the intermediation of the ventral ganglia as reflex centers.

These results were confirmed by Maxwell (83), Biedermann (7), and Morgulis (87). Maxwell stated that the coordination observed in *Lumbricus* after the cord is transected does not occur in the polychaete, *Nereis*. Biedermann emphasized the loss of tonus in segments lacking the nerve cord. Moore (85) and Garrey and Moore (39) experimentally supported Friedländer's theory of the origin of the peristaltic contractions. Moore elicited peristalsis by hanging weights to a suspended earthworm in which the epidermal receptors had been anaesthetized. Garrey and Moore stroked preparations of earthworms, which were held by clamps to minimize tension, with a brush and maintained that peristaltic waves are induced by backward strokes but are inhibited by forward strokes. They concluded that contact with the substratum as well as tension from segment to segment is of importance in initiating peristalsis. They stated, however, that in these clamped specimens coordinated waves cease when the nerve cord is cut and that the type of response varies with the direction of propagation of the impulse in the nerve cord. Knowlton and Moore (67) further developed the idea of reciprocal innervation of the two muscle layers which

had been suggested by Friedländer and found that when a worm is suspended in strychnine sulphate, both muscle layers contract; hence an impulse which normally causes relaxation is converted into an excitation.

Bovard (13) supported Friedländer's observation of coordination between muscles anterior and posterior to segments lacking the nerve cord. When, however, he pinned the denervated segments down to eliminate pull from one region to the other, he found, as did Garrey and Moore, no coordination of a contraction wave. Hess (52) and Janzen (63) opposed the latter statement and attributed coordination to conduction in the peripheral plexus. Janzen claimed that the net can conduct in all directions in response to stimulation, but that it is normally under central regulation. Hess said that impulses can be transmitted in this plexus through six segments in response to mechanical and through fifteen segments in response to thermal stimulation. The author repeated this experiment with results which support Bovard and Garrey and Moore; it seems probable that Hess observed random movements on opposite sides of the clamped denervated region.

Coonfield (25) brought important evidence against the idea of non-polarized conduction in the peripheral plexus. He studied the function of the network with respect to the control of liberation of mucous and coelomic fluid by the epidermal glands and dorsal pores. He obtained only local secretion when he stimulated a region lacking the nerve cord but secretion over a considerable area when he stimulated a normal region. He concluded that the subepidermal plexus is not a non-polarized nerve net.

The converse of the operations just described is to anaesthetize or remove the muscles from part of the body of a worm, leaving only the nerve cord functional. Biedermann (7) was the first to do this. In 1904 he observed that coordination occurs between the muscles of two regions joined only by the nerve cord. He postulated that all conduction of impulses is by means of the nervous system. Bovard (13) repeated this experiment with the same results and observed that impulses pass through an intact region of an earthworm which is pinned down to prevent tension or one in which the muscles are anaesthetized until the nerve cord is cut or blocked by a drug such as stovaine. He maintained that impulses die out in an exposed strip of the nerve cord more rapidly than when the tissues are intact, and he postulated segmental reenforcement under the latter condition.

It is agreed, therefore, by all of the investigators concerned that conduction of impulses in locomotion can occur by means of the isolated nerve cord and that coordination usually occurs anterior and posterior to a region lacking the nerve cord if movement in this region is unrestricted. It is not agreed, however, whether this coordination is due to stimulation by tension and surface contact or to non-polarized conduction in the peripheral plexus. Coonfield's evidence that the subepidermal plexus does not function as a freely conducting net in epithelial secretion appears conclusive. This does not necessarily apply to the intermuscular plexus, but it seems probable that the two, being part of the same general system, should function in the same way. Friedländer's observation that a forward moving wave does not cross a denervated strip and his observation of coordination between two regions connected by a thread support this conclusion that the plexus is not a net.

The failure of Garrey and Moore and of Bovard to observe coordination across a

cut in the nerve cord when the effect of tension is eliminated and the fact that no contractions occur in the segments lacking the cord are further evidence against the conduction of locomotor impulses by the peripheral plexus. The reasonable conclusion is that coordination occurs between two parts of an earthworm separated by segments lacking the nerve cord, but that it is due to passive pull of this region and subsequent stimulation of intermuscular receptors which set up the reciprocal reflex of the peristaltic wave.

In addition to these experiments in which only one region of a worm has been partially demobilized, other preparations have been made of parts of specimens from which the nerve cord has been entirely removed. Fürst (38) and Straub (124) found spontaneous contractions and responses to electrical stimulation in muscle-skin preparations from which the nerve cord had been removed. Straub suspended such preparations and observed spontaneous contractions in the longitudinal muscles at the rate of approximately four per minute, and shorter, more rapid contractions in the circular muscles. He found strong responses of both muscle layers to electrical stimulation or to stretching and contended that these contractions are not entirely eliminated by curare. He postulated myogenic contraction and spontaneity of movement in the musculature in the earthworm. Buddington (17) made similar preparations but could obtain no spontaneous movement such as that found by Straub unless small pieces of the nerve cord were left in the preparation. He did, however, obtain characteristic contractions in response to electrical stimulation. Buddington's results were, in general, confirmed by Bovard (13), but he apparently did not suspend his specimens. Hart (45) graphically registered spontaneous movements in suspended preparations lacking the nerve cord and said that failure to obtain such movements may have been due to the use of short pieces.

Janzen (63) observed spontaneous movements in ten of eighteen muscle-skin preparations. When he applied strong doses of curare or ether, the spontaneous contractions and spread of responses to mechanical stimulation were either absent or present only to a slight degree. Only the response of the muscle fibers to direct stimulation persisted.

All of the above investigators, therefore, agree that strips of the earthworm lacking the nerve cord, like other muscle preparations, respond to direct stimulation. Spontaneous contractions were observed in such preparations by all but one (Buddington) who suspended them but not by those who left the preparations resting in the horizontal position. It appears likely, as Hart suggested, that spontaneous movements in preparations lacking the nerve cord occur only when relatively long pieces are suspended. This indicates that the peristalsis is initiated by tension on the muscles through the proprioceptors which Dawson (27) described on the nerve rings and is, therefore, really a response rather than spontaneous movement. The ease with which spontaneous movements arise in specimens with the nerve cord present indicates that the ganglia give out motor impulses when there is little or no peripheral stimulation. The experiments with curare and ether indicate conclusively that the peristalsis in the earthworm, unlike most smooth muscle preparations, requires the presence of peripheral nervous tissue.

These observations as well as those presented above concerning conduction in a region lacking the nerve cord indicate that no conclusions can be drawn concerning the function of the peripheral

plexus except that it does not function as a true net in the coordination of peristaltic movement and in epithelial secretion. It probably functions, as Smallwood (117) suggested, as a center of branching of processes to the sensory cells.

The study of the earthworm has also contributed to the problem of segmental independence. In 1897 Maxwell (83) observed a lack of tonus in segments from which the ganglia had been removed and suggested that each ganglion is a local motor center for its particular segment. The importance of tonus as controlled by the ganglia was emphasized in a discussion of crawling by Van Essen (130). Several investigators, Friedländer (35 and 37), and Knowlton and Moore (67) developed the idea of reciprocal contraction of longitudinal and circular muscles in crawling, and Buddenbrock (16) postulated a bisegmental reflex involving two consecutive ganglia to account for this movement.

Janzen (63), by a series of operations, obtained evidence that each ganglion is a reflex center for the antagonistic contraction of the two muscle layers and for the movement of the setae in any given segment. He asserted, however, that the reflexes of any particular segment are coordinated with those of the segments immediately anterior and posterior to it and that the control is usually homolateral, but that impulses can cross from side to side. It may be concluded from this evidence concerning ganglionic effects on tonus and on segmental reflexes that each segment is essentially an equipotential but not an independent unit.

The results obtained in observations on the rate of conduction in the nerve cord differ considerably. Bovard (12) by means of myographs ascertained the rate of conduction in the motor fibers of the cord to be approximately 0.025 m. per second and that in the giant fibers to be approximately 1.25 m. per second. Lapique and Veil (76) by the same method found conduction in the ventral nerve cord at the rate of 0.6 m. per second, and in the muscles at 0.35 m. per second. More recently Eccles, Granit and Young (29) measured the conduction rate in the giant fibers by means of action potentials. They found two groups of impulses, one at the rate of 17 to 25 m. per second and the other at 0.7 to 1.2 m. per second.

Conduction in the giant fibers differs from that in the rest of the nerve cord. When strongly stimulated, earthworms swing the two ends together in a sort of coil and then apart vigorously. Friedländer (37) suggested that, since these quick end-to-end contractions are lacking when the cord is cut, the control of such contractions is the function of the giant fibers. Rabes (104), however, claimed that end-to-end contractions can occur before regeneration of the giants is complete. Bovard (14) found that when the cord is transected, the giant fibers regenerate later than the fibers concerned with normal locomotion and that the action of the giants can be stopped by stovaine without affecting that of the bulk of the fibers in the cord. He concluded that the giant fibers are not associated with normal locomotion but with rapid impulses involved in responses of the entire animal. Yolton (137) cut the dorsal giant fibers while the rest of the cord was left intact and found a loss of these quick end-to-end contractions. Single giant fibers were cut by Stough (123) who maintained that the median dorsal giant fiber of *Lumbricus* conducts postero-anteriorly while the two lateral ones conduct antero-posteriorly. Eccles, Granit, and Young (29) studied the action potentials in the giants instead of muscular activity. They disagreed with Stough by stating that these fibers

can conduct in either direction and that apparently the slow impulse mentioned above travels in the lateral fibers and the fast one in the median giant fiber. Prosser (100) found that in embryos of *Eisenia*, the end-to-end contractions do not appear until after a giant fiber is differentiated. It may be concluded that the giant fibers conduct rapid impulses which are involved in rapid contraction of both ends of the earthworm. Whether they are polarized or not requires further investigation.

The problem of cephalic dominance is also of importance in the physiology of the nervous system of the earthworm. Histological as well as functional evidence indicates that the ventral nerve cord is largely motor and the brain sensory in function. Janzen (63) claimed that removal of the cerebral ganglion interferes very little, if at all, with most motor activities, but that motor centers exist in the ventral ganglia, their effect being strongest in the subpharyngeal ganglion and decreasing posteriorly. He says, for example, that behavior when the anterior end is hung over the edge of a plate is largely controlled by the subpharyngeal ganglion.

Friedländer (37) found that brainless worms are restless and active, that they crumple the anterior tip, burrow very reluctantly, but enter into coitus, and crawl normally. Yerkes (136) and Heck (48) taught earthworms to run simple "T" mazes. They found that when the first four segments were removed, the ability to run the maze was retained. Focke (32) said that when the brain is removed, an earthworm swings its head about more than usually, turns over normally when placed on its dorsal side, and burrows into the substratum but requires thirty minutes to burrow as contrasted with two minutes normally. These effects indicate slight sensory deficiency resulting from loss of the brain and no interference with motor activity.

The effect of the brain on responses to light has been more thoroughly investigated. Graber (41), Loeb (82), and Hesse (55) stated that when the anterior four or five segments are removed, earthworms aggregate in the dark regions of a box nearly as frequently as do normal worms. In 1924 Hess (50) maintained that when the brain is removed from *Lumbricus* the responses to light of moderate intensity are reversed from negative to positive. Nomura (92) obtained similar results with *Eisenia*. Prosser (101) found that separation of the two lobes has nearly the same effect upon responses to light in *Eisenia* as does removal of the brain, and that subjection to low temperatures or injection of depressant drugs over the brain also have essentially the same effect. He concluded that normally the tracts involved in this response cross from one side of the brain to the other and that this crossing-over may explain the reversal on removal of the transverse tracts.

It may be concluded that physiological studies of the nervous system of the earthworm do not completely support the conclusions concerning function drawn from morphological observations. The functions of the peripheral plexus are still uncertain, although it is probably largely sensory in nature. Physiological evidence does not support the idea that the subepidermal plexus is a non-polarized nerve net. The evidence of Eccles, Granit and Young concerning rapid conduction in both directions in the giant fibers does not support Stough's conception of segmental synapses in them. It is certain that the ventral ganglia are largely motor and the brain is almost entirely sensory, but quantitative measurements of such effects are entirely lacking. It has been demonstrated that there is antagonism

between circular and longitudinal muscles, but very little is known concerning the mechanism involved.

In conclusion, although the earthworm has contributed to many problems of invertebrate neurology, at least three general problems have been treated more conclusively in the earthworm than in other animals. It was stated above that most of the histological evidence indicates that the peripheral plexus of the earthworm is a true nerve net with continuity of fibers. The functional evidence, however, strongly indicates that the peripheral plexus does not function as a nonpolarized net, at least not with respect to the impulses involved in epithelial secretion and in coordinated muscular contraction. Thus, the nerve cord is essential to normal locomotion, and Friedländer is fully supported in his postulate of reciprocal reflex contractions of both muscle layers resulting from stimulation by tension and contact. On the other hand, some reactions appear to be under peripheral control. The importance of peripheral receptors is indicated by coordination anterior and posterior to a region lacking the nerve cord and by the responses of muscle-skin preparations. It is probable that these peripheral receptors are connected with the muscles both by fibers originating in the peripheral plexus and by others from the segmental nerves. It appears, therefore, that the earthworm falls between the polychaetes, in which the central nervous system controls peristaltic contractions, and the flatworms, in which peripheral elements are more important.

The earthworm has contributed more than other forms to a second important problem,—the structure and function of the giant fibers. According to the above evidence these fibers are unlike most others structurally and functionally. These big myelinated bundles of axones have abundant connections with cells, with the neuropile, and with each other. They conduct rapid impulses involved in defensive reactions of the entire animal, and there is coordination not only throughout each giant trunk but also between the two lateral fibers. Apparently these giant fibers lack the segmental independence of most neurones of the cord, yet segmental septa indicate that each fiber is not one long axone extending the entire length of the worm. The function of these segmental septa is an important problem for the future.

The earthworm is one of the simplest forms in which cephalic dominance in the central nervous system has been clearly demonstrated. The distribution of nerves in the anterior segments indicates fusion of the ganglia of the first three segments. The subpharyngeal ganglion is important in regulating the motor activities of the rest of the cord. The brain is a sensory center and controls some types of behavior of the earthworm such as the responses to light.

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LIST OF LITERATURE

(1) Anderson. Nervous Systems *in* Todd's Cyclopaedia of Anatomy and Physiology. III. *London*. 1839.

(2) Apathy, S. Das leitende Element des Nervensystems und seine topographische Beziehungen zu den Zellen. *Mit. a. d. Zool. Sta. zu Neapel*, 12: 495–748. 1897.

(3) Bailey, P. L. Influence of the nervous system in the regeneration of *Eisenia foetida*, Sav. *Jour. Exp. Zool.*, 57: 473–509. 1930.

(4) Beddard, F. E. A Monograph of the Order of Oligochaeta. 769 pp. Clarendon Press, *Oxford*. 1895.

(5) Benham, W. B. Studies on earthworms. *Quart. Jour. Mic. Sci.*, 26: 213–301. 1886.

(6) Bialkowska, W., and Z. Kulikowska. Über den Golgi-Kopschen Apparat der Nervenzellen bei den Hirudineen und *Lumbricus*. *Anat. Anz.*, 38: 193–207. 1911.

(7) Biedermann, W. Studien zur vergleichenden Physiologie der peristaltischen Bewegungen. *Pflüg. Arch.*, 102: 475–542. 1904.

(8) Blanchard, E. Du système nerveux chez les Invertébrés. (Mollusques et Annelés) dans ses rapports avec la classification de ces animaux. *Comptes Rend.*, 27: 623–625. 1848.

(9) Boulé, L. L'impregnation des éléments nerveux du Lombric par le nitrate argent. *Le Névraxe*, 9: 313–327. 1907.

(10) ———. Recherches sur le système nerveux central normal du Lombric. *Le Névraxe*, 10: 13–58. 1908.

(11) ———. Nouvelles recherches sur le système nerveux central normal du Lombric. *Le Névraxe*, 15: 425–467. 1913.

(12) Bovard, J. F. Giant fibers and normal transmission by the nerve cord of earthworms. *Science*, 42: 620. 1915.

(13) ———. The transmission of nervous impulses in relation to locomotion in the earthworm. *Univ. Cal. Pub. in Zool.*, 18: 103–134. 1918.

(14) ———. The function of the giant fibers in earthworms. *Univ. Cal. Pub. in Zool.*, 18: 135–144. 1918.

(15) Bozler, E. Untersuchungen über das Nervensystem der Coelenteraten I. Kontinuität oder Kontakt zwischen den Nervenzellen. *Zeit. f. Zellforsch. u. Mik. Anat.*, 5: 244–262. 1927.

(16) Buddenbrock, W. v. Grundriss der vergleichenden Physiologie. Erster Teil, Sinnesorgane und Nervensystem. 1924.

(17) Buddington, R. A. Some physiological characteristics of Annelid muscle. *Am. Jour. Physiol.*, 7: 155–179. 1902.

(18) Cajal, S. R. Neuroglia y neurofibrillas del *Lumbricus*. *Trab. del Labor. Invest. Biol. de la Univ. de Madrid*, 3: 277–285. 1904.

(19) Cerfontaine, P. Recherches sur le système cutané et sur le système musculaire du *Lombric terr. Archives de Biol.*, 10: 327–428. 1890.

(20) ———. Contribution à l'étude du système nerveux central du *Lombric terrestre*. *Bull. de l'Acad. roy. de Belgique*, Sér. 3, 23: 742–752. 1892.

(21) Chen, T. T. Sympathetic nervous system of an Annelid. Master's essay. Oberlin College. 1930.

(22) Claparède, E. Histologische Untersuchungen über den Regenwurm. *Zeit. f. wiss. Zool.*, 19: 563–625. 1869.

(23) Clarke, J. L. On the nervous system of *Lumbricus terrestris*. *Proc. Roy. Soc. London*, 8: 343–351. 1856.

(24) Combs, S. Importanza della fibre della glia per spiergare il meccanismo di movimento nei Lombricidi. *Atti. Acc. Gioenia Catania*, 5: 8. 915.

(25) Coonfield, B. R. The peripheral nervous system of earthworms. *Jour. Comp. Neur*, 55: 7–17. 1932.

(26) Cuvier, M. Le Règne Animal. II: 528. 1817.

(27) Dawson, A. B. The intermuscular nerve cells of the earthworm. *Jour. Comp. Neur.*, 32: 155–171. 1920.

(28) Dechant, E. Beiträge zur Kenntnis des peripheren Nervensystems des Regenwurmes. *Arb. d. Zool. Inst. Wien*, 16: 361–383. 1906.

(29) Eccles, J. C., R. Granit, and J. Z. Young. Impulses in the giant nerve fibers of earthworms. *Jour. Physiol.*, 77: 23P–25P. 1933.

(30) Faivre, E. Études sur l'histologie comparée du système nerveux. Part I. *Ann. des Sci. Nat.*, 5: 337–374. 1856. Part II. *Ibid.*, 6: 16–82. 1856.

(31) Fling, H. R. A contribution to the nervous system of the earthworm. *Jour. Comp. Neur.*, 8: 230–232. 1898.

(32) Focke, F. Experimente und Beobachtungen über die Biologie des Regenwurms, unter besonderer Berücksichtigung der Frage nach der Raumorientierung. *Zeit. f. Wiss. Zool.*, 136: 376–421. 1930.

(33) Fortuyn, A. B. D. Vergleichende Anatomie des Nervensystems. Erst. Teil. Die Leitungsbahnen im Nervensystem der Wirbellosen Tiere. Bohn. 1920.

(34) Friedländer, B. Beiträge zur Kenntnis des Centralnervensystems von *Lumbricus*. *Zeit. f. Wiss. Zool.*, 47: 47–85. 1888.

(35) ———. Über das Kriechen der Regenwürmer. *Biol. Zentralbl.*, 8: 363–366. 1888.

(36) ———. Altes und Neues zur Histologie des Bauchstranges des Regenwurms. *Zeit. f. Wiss. Zool.*, 58: 661–693. 1894.

(37) ———. Beiträge zur Physiologie des Zentralnervensystems und der Bewegungsmechanismus der Regenwürmer. *Pflüg. Arch.*, 58: 168–207. 1894.

(38) Fürst, M. Zur Physiologie der glatten Muskeln. *Pflüg. Arch.*, 46: 367–382. 1890.

(39) Garrey, W. E., and A. R. Moore. Peristalsis and coördination in the earthworm. *Am. Jour. Physiol.*, 39: 139–148. 1915.

(40) Goldfarb, A. J. The influence of the nervous system in regeneration. *Jour. Exp. Zool.*, 7: 643–722. 1909.

(41) Graber, V. Fundamentalversuche über die Helligkeitsund Farbenempfindlichkeit augenloser und geblendeter Thiere. *Sitzungs. der K. Akad. der Wiss. Wien*, Abt. I, 87: 201–236. 1882.

(42) Hall, A. R. Regeneration in the Annelid nerve cord. *Jour. Comp. Neur.*, 33: 163–178 1921.

(43) Haller, B. Beiträge zur Kenntniss der Textur des Centralnervensystems höher Würmer. *Arb. Zool. Inst. Wien*, 8: 175–312. 1889.

(44) ———. Über das Bauchmark. *Jenaische Zeit. für Naturwiss.*, 46: 591–632. 1910.

(45) Hart, P. C. L'action des ions Na, K, et Ca et du nitrate d'uranyle sur les mouvements rhythmiques spontanés du sac musculo-cutané du lombric. *Arch. Néerland. de Physiol.*, 9: 1–29. 1924.

(46) Havet, J. Structure du système nerveux des Annélides. *La Cellule*, 17: 63–137. 1900.

(47) Havet, M. R. Relations de la neuroglie avec l'appareil vasculaire chez les Invertébrés. *Comptes Rendus Acad. des Sci.*, 162: 568–570. 1916.

(48) Heck, L. Über die Bildung einer Assoziation beim Regenwurm auf Grund von Dressurversuchen. *Lotos (Deutsch. Naturwiss. verein.) Prague*, Nos. 67–68: 168–189. 1919–20.

(49) Hescheler, K. Über Regenerationsvorgänge bei Lumbricideen. *Jenaische Zeit. f. Naturwiss.*, 31: 521–605. 1898.

(50) Hess, W. N. Reactions to light in the earthworm, *Lumbricus terrestris*, L. *Jour. Morph. and Physiol.*, 39: 515–542. 1924.

(51) ———. Nervous system of the earthworm, *Lumbricus terrestris*, L. *Jour. Morph. and Physiol.*, 40: 235–261. 1925.

(52) ———. The nerve plexus of the earthworm, *Lumbricus terrestris*. *Anat. Rec.*, 31: 335–336. 1925.

(53) ———. Photoreceptors of *Lumbricus terrestris* with special reference to their distribution, structure, and function. *Jour. Morph. and Physiol.*, 41: 63–95. 1925.

(54) Hesse, R. Zur vergleichenden Anatomie der Oligochaeten. *Zeit. f. Wiss. Zool.*, 58: 394–439. 1894.

(55) ———. Untersuchungen über die Organe der Lichtempfindung bei niederen Tieren. I. Die Organe der Lichtempfindung bei Lumbriciden. *Zeit. f. Wiss. Zool.*, 61: 393–419. 1896.

(56) Holmes, M. T. The connective tissue structure of the ganglion of the earthworm, *Lumbricus terr. Jour. Comp. Neur.*, 51: 393–408. 1930.

(57) Home, E. On the internal structure of the human brain when examined in the microscope, as compared with that of fishes, insects and worms. Croonian Lecture. *Proc. Roy. Soc. Lond.*, 114: 1–10. 1824.

(58) Hönig, J. Die Neurochorde des *Criodrilus Lacuum*, Hoffm. *Arb. Zool. Inst. Wien.* 18: 257–282. 1910.

(59) Horst, R. Aanteekeningen op de Anatomie van *Lumbricus terrestris*, L. *Tijd. nederl. dierk. Vereen.*, 3: 37–68. 1878.

(60) ———. Die Lumbricidenhypodermis. *Tijd. nederl. dierk. Vereen.*, 4: 56. 1879.

(61) Hunt, H. R. Regenerative phenomena following the removal of the digestive tube and the nerve cord of earthworms. *Mus. Comp. Zool. Harv.*, 62: 571–581. 1919.

(62) Imai, T. Nervous system of the earthworm, *Perichaeta mcg.* I. Gross anatomy of the nervous system. *Tok. Univ. Sci. Rep.*, 3: 443–461. 1928.

(63) Janzen, R. Beiträge zur Nervenphysiologie der Oligochaeten. *Abt. f. All. Zool. u. Phys. der Tiere*, 50: 51–150. 1931.

(64) Joseph, H. Zur Kenntnis der Neuroglia. *Anat. Anz.*, 11: 354–357. 1900.

(65) ———. Untersuchungen über die Stutzsubstanzen des Nervensystems. *Arb. Zool. Inst. Univ. Wien*, 13: 335–400. 1902.

(66) Keyl, F. Beiträge zur Kenntnis von *Branchium sowerbyi*, Bedd. *Zeit. f. wiss. Zool.*, 107: 199–308. 1913.

(67) Knowlton, F. P., and A. R. Moore. Note on the reversal of reciprocal inhibition in the earthworm. *Amer. Jour. Physiol.*, 44: 490–491. 1917.

(68) Kolmer, W. Über das Verhalten der Neurofibrillen an der Peripherie. *Anat. Anz.*, 26: 560–569. 1905.

(69) Kowalski, J. De l'impregnation par la méthode à l'argent de Cajal des neurofibrilles du *Lumbricus* consécutivement à l'action du froid. *Soc. Sci. phys. et nat. Bordeaux*, 16–18. 1907.

(70) ———. Contribution à l'étude de neurofibrilles chez le Lombric. *La Cellule*, 25: 291–346. 1909.

(71) KRAWANY, J. Untersuchungen über das Zentralnervensystem der Regenwürmer. *Arb. Zool. Inst. Wien*, 15: 281–316. 1905.

(72) KROPP, B. Brain transplantation in regenerating earthworms. *Jour. Exp. Zool.*, 1933.

(73) LANGDON, F. E. The sense organs of *Lumbricus agricola*, Hoffm. *Jour. Morph. and Physiol.*, 11: 193–232. 1895.

(74) ———. Sense organs of *Lumbricus agricola*, Hoffm. *Anat. Anz.*, 10: 114–117. 1895.

(75) LANKESTER, E. R. Anatomy of the earthworm. Part III. *Quart. Jour. Micr. Sci.*, N. S. 5: 99–116. 1865.

(76) LAPIQUE, M., and C. VEIL. Vitesse de conduction nerveuse et musculaire comparée à la chronaxie chez la Sangue et le Ver de terre. *Comp. Rend. Soc. Biol.*, 93: 1590–1591. 1925.

(77) LENHOSSÉK, M. VON. Ursprung, Verlauf, und Endigung der sensibeln Nervenfasern bei *Lumbricus*. *Archiv. f. Mikr. anat.*, 39: 102–137. 1892.

(78) LEO, J. De structura *Lumbrici terrestris*. *Isis von Oken*, Jahrgang 1822 (erster Band) col. 492–497. 1822.

(79) LEYDIG, F. Über das Nervensystem der Anneliden. *Müll. Arch. f. Anat. Phys. u. wiss. Med.*, 90–129. 1862.

(80) ———. Vom Bau des Thierischen Körpers. 278 S. *Tübingen*. 1864.

(81) ———. Die riesigen Nervenröhren im Bauchmark der Ringelwürmer. *Zool. Anz.*, 9: 591–597. 1886.

(82) LOEB, J. Beiträge zur Gehirnphysiologie der Würmer. *Pflüg. Arch.*, 56: 247–269. 1894.

(83) MAXWELL, S. S. Beiträge zur Gehirnphysiologie der Anneliden. *Pflüg. Arch.*, 67: 263–297. 1897.

(84) MOJSISOVICS, A. VON. Zur Lumbricidenhypodermis. *Zool. Anz.*, 2: 89–91. 1879.

(85) MOORE, A. R. Muscle tension and reflexes in the earthworm. *Jour. Gen. Physiol.*, 5: 327–333. 1923.

(86) MORGAN, T. H. Experimental studies of the internal factors of regeneration in the earthworm. *Arch. f. Entwicklungs.*, 14: 562–591. 1902.

(87) MOROULIS, S. The movements of the earthworm: a study of a neglected factor. *Jour. Comp. Neurol.*, 20: 615–624. 1910.

(88) MORREN. Histoire du *Lombric terrestre*. *Bruxelles*. 116 pp. 1829.

(89) NANSEN, F. Die Struktur und wechselseitige Beziehung der histologischen Elemente des Zentralnervensystems. (Reviewed by Obersteiner.) *Biol. Cent.*, 8: 93–96. 1888.

(90) NANSEN, F. The Structure and Combination of the Histological Elements of the Central Nervous System. *Bergen*. 217 pp. 1887.

(91) NEWPORT, G. On the reproduction of lost parts in the earthworm. *Proc. Lin. Soc.*, 2: 256. 1855.

(92) NOMURA, E. Effect of light on the movements of the earthworm, *Allolobophora foetida*, Sav. *Tohoku Univ. Sci. Rep.*, Ser. 4, 1: 294–409. 1926.

(93) NUZUM, M. F., and H. W. RAND. Can the earthworm pharynx epithelium produce central nervous tissue? *Biol. Bull.*, 47: 213–222. 1924.

(94) OGAWA, F. On the number of ganglion cells and nerve fibers of the ventral nerve cord of the earthworm. I. The number of ganglion cells. *Tohoku Imp. Univ. Sci. Rep.*, Ser. 4, 3: 745–756. 1928.

(95) ———. On the number of ganglion cells and nerve fibers of the ventral nerve cord of the earthworm. II. The number of nerve fibers. *Tohoku Imp. Univ. Sci. Rep.*, Ser. 4, 5: 691–716. 1930.

(96) PERRIER, E. Recherches pour servir à l'histoire des *Lumbricus terrestris*. *Nouvelles Archives du Muséum d'Histoire naturelle de Paris*, 18: 5–198. 1872.

(97) ———. Études sur l'organisation des *Lombriciens terrestres*. *Arch. de Zool. expér.*, 3: 331–530. 1874.

(98) ———. Études sur l'organisation des *Lombriciens terrestres*. *Arch. de Zool. expér.*, 9: 175–248. 1881.

(99) PFLÜCKE, M. Zur Kenntnis des feineren Baues der Nervenzellen bei Wirbellosen. *Zeit. f. wiss. Zool.*, 60: 500–542. 1895.

(100) PROSSER, C. L. Correlation between development of behavior and neuromuscular differentiation in embryos of *Eisenia foetida*, Sav. *Jour. Comp. Neurol.*, 58: 603–641. 1933.

(101) ———. Effect of the central nervous system on responses to light in *Eisenia foetida*, Sav. *Jour. Comp. Neurol.*, 59: 61–91. 1934.

(102) DE QUATREFAGES, M. A. Note sur l'anatomie des sangues et des lombrics. *Ann. Sci. Nat.*, Sér. 3, 8: 36. 1847.

(103) ———. Études sur les types inférieurs de l'embranchement des Annelés. *Ann. Sci. Nat.*, Sér. 3, 18: 167–179. 1852.

(104) RABES, O. Über Transplantationsversuche an Lumbriciden. *Biol. Zent.*, 21: 633–650. 1901.

(105) Rand, H. W. Regenerating nervous system of *Lumbricidae* and the centrosome of its nerve cells. *Mus. Comp. Zool. at Harvard College*, 37: 85–163. 1901.

(106) ———. The behavior of the epidermis of the earthworm in regeneration. *Arch. f. Entwick.*, 19: 16–57. 1904.

(107) Retzius, G. Das Nervensystem der Lumbricinen. *Biol. Unters.*, N. F. 3: 1–16. 1892.

(108) ———. Die Smirnowschen freien Nervenendigungen im Epithel des Regenwurms. *Anat. Anz.*, 10: 117–123. 1895.

(109) Rogers, C .G. Textbook of Comparative Physiology. 635 pp. McGraw-Hill. *New York*. 1927.

(110) Robin, J. On the anatomy of the nervous system in the earthworm, *Lumbricus terrestris*. *Quart. Jour. Micr. Sci.*, N. S. 3: 106–109. 1863.

(111) Roth. De animalium invertebratorum systemati nervoso. Diss. inaug. *Vicburgi*. 1825.

(112) Schneider, K. C. Histologisches Praktikum der Tiere. 615 pp. *Jena*. 1908.

(113) Schwartz, H. G. Studies in the regeneration of central nervous tissues. I. Origin of nerve cells in regenerated cerebral ganglion in the earthworm. *Jour. Comp. Neur.*, 55: 545–572. 1932.

(114) Sigmund, G. Die Bedeutung des Nervensystems bei der Regeneration, untersucht an *Eisenia. Biol. Gen.*, 4: 337–350. 1928.

(115) Smallwood, W. M. The nerve net in the earthworm. *Proc. Nat. Acad. Sci.*, 9: 95–100. 1923.

(116) ———. Further discussion of the nerve net in the earthworm. *Anat. Rec.*, 26: 347. 1923.

(117) ———. The peripheral nervous system of the common earthworm, *Lumbricus terrestris*. *Jour. Comp. Neur.*, 42: 35–55. 1926.

(118) ———. The nervous structure of the annelid ganglion. *Jour. Comp. Neur.*, 51: 377–393. 1930.

(119) Smallwood, W. M., and M. T. Holmes. The neurofibrillar structure of the giant fibers in *Lumbricus terrestris* and *Eisenia foetida*. *Jour. Comp. Neur.*, 43: 327–345. 1927.

(120) Smirnow, A. Über die Nervenendigungen im Epithel des Regenwurms. *Anat. Anz.*, 9: 570–578. 1894.

(121) Stephenson, J. The Oligonchaeta. 978 pp. Clarendon Press. *Oxford*. 1930.

(122) Stough, H. B. Giant nerve fibers of the earthworm. *Jour. Comp. Neur.*, 40: 409–463. 1926.

(123) Stough, H. B. Polarization of the giant nerve fibers of the earthworm. *Jour. Comp. Neur.*, 50: 217–230. 1930.

(124) Straub, W. Zur Muskelphysiologie des Regenwurms. *Pflüg. Archiv*, 79: 379–400. 1900.

(125) Szüts, A. von. Über die Ganglienzellen der Lumbriciden. *Anat. Anz.*, 42: 262–269. 1912.

(126) ———. Studien über die feinere Beschaffenheit des Nervensystems des Regenwurms, nebst Bemerkungen über die Organisierung des Nervensystems. *Archiv. f. Zellforsch.*, 13: 270–317. 1915.

(127) Tuge, H. On the number of ganglion cells in the suprapharyngeal ganglion and in the XXX ventral ganglion of the earthworm, *Pheretima megascolidioides*, G and H. *Tohoku Imp. Univ. Sci. Rep.*, Ser. 4, 4: 597–602. 1929.

(128) Ude, H. Über die Rückenporen der terricolen Oligochaeten, nebst Beiträgen zur Histologie des Leibesschlauches und zur Systematik der Lumbriciden. *Zeit. f. wiss. Zool.*, 43: 87–148. 1886.

(129) d'Udekem, M. Mémoire sur les Lombricins. *Nouveaux Mém. de l'Acad. roy. des Sci., Lettres, et Beaux-Arts de Bruxelles*, 35: 1–44. 1865.

(130) Van Essen, J. Über das Kriechen der Regenwürmer. *Zeit. f. vergl. Physiol.*, 15: 389–411. 1931.

(131) Vejdovsky, F. System und Morphologie der Oligochaeten. *Prag*. 166 pp. 1884.

(132) Vignal, W. Recherches histologiques sur les centres nerveux de quelque invertébrés. *Arch. d. Zool. exp. et gén.*, Sér. 2, 1: 267–412. 1883.

(133) Walter, G. Mikroscopische Studien über das Centralnervensystem wirbelloser Thiere. *Bonn*. 56 pp. 1863.

(134) Williams, T. Report on the British Annelida. *Rep. of Brit. Assoc. for Adv. of Sci.*, Report for year 1851, p. 159.

(135) Willis. De anima brutorum. 1672.

(136) Yerkes, R. M. The intelligence of earthworms. *Jour. Animal Behavior*, 2: 332–352. 1912.

(137) Yolton, L. W. The effects of cutting the giant fibers in the earthworm, *Eisenia foetida*, Sav. *Proc. Nat. Acad. Sci.*, 9: 383–385. 1923.

(138) Zyeno, D. H. Distribution of intermuscular nerve cells in the earthworm. *Tohoku Imp. Univ. Sci. Rep.*, Ser. 4, 5: 449–466. 1930.

THE HABITS AND CHARACTERISTICS OF NOCTURNAL ANIMALS

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A CONSIDERATION of problems associated with the nocturnal activity of animals tends to become as complicated as it is interesting. The contributions of several branches of biological investigation must be drawn together before even a fairly complete picture appears. This discussion of the conditions of life at night, the possible advantages of the nocturnal habit, and the usefulness at night of the several senses follows records of the writer ('31, '32, '33), Park, *et al.* ('31, '32) and many others on the nocturnal and crepuscular activity of various animals. In the interest of brevity references are cited only in connection with newer, more controversial or more significant phases of the discussion. In general, the study is limited to a consideration of the arthropods and land vertebrates, although some other references are made.

A. ENVIRONMENTAL FACTORS

Park and his colleagues ('31) determined for several Ohio insects of climax forests, that for the species studied, and within the limits of the ranges of the factors observed, nocturnal activity tended to increase with the increase of relative humidity, decrease of air temperature and rate of evaporation. Conversely, nocturnal activity tended to decrease with decreased relative humidity, increase of air temperature and rate of evaporation. Similarly Necheles ('27) reports that the only factor which has any appreciable influence on the nocturnal activity of certain cockroaches and mosquitoes is air humidity, as influenced by temperature, and its effect on the rate of water loss by these insects. The value of increased humidity to nocturnal animals receives comment below. Nevertheless, at least for vertebrate animals the absence of light looms as the most characteristic factor of the nocturnal environment.

The influence of light is apparent in most animal forms. Diurnal insects accustomed to sleep at night are less active or are quiescent on cloudy days. Conversely, nocturnal forms shun the light. Moonlight tends to enliven diurnal forms at night to some extent. Thus, we have the calling of day birds and the voicing of some primarily daytime mammals at night. The phenomenon of phototropism is quite familiar. Most butterflies are attuned to a high intensity of light, many moths to a low intensity, so that bright sunlight, which calls forth the one, causes the other to retreat; and on the other hand a light like that of the candle, so weak as not to stimulate a butterfly, produces a marked response in the moth. Rau ('29, '32) reports for saturniid moths and two firefly species that normal activity is brought about by certain intensities of light, and that these animals respond at other than the usual times if the optimum light conditions are simulated. *Samia cecropia* is reported to fly regularly during the hour just before and during the period of dawn; *Platysamia cynthia* and *Telea polyphemus* to have a period of flight in the hours before midnight and another at

dawn; *Callosamia promethea* to fly in the late afternoon. *Photinus pyralis* is reported to fly early and in low flight, *Photuris pennsylvanica* to fly only after dark and at higher levels. Allard ('31) notes that the general trend of the curve of relative humidity may be accidentally associated with that of the sunset curve. He believes the activity of fireflies to be determined by a more or less specific level of light intensity operating through the visual sense.

B. POSSIBLE ADVANTAGES OF THE NOCTURNAL HABIT

In considering the reason for the activity of certain forms at night while the greater part of the animal world sleeps, there appear certain probable advantages which may or may not constitute sufficient reasons for the adoption of the nocturnal habit. It would not be supposed that, except in the higher mammals, the night time is consciously chosen on account of any of these advantages. It might be considered that these benefits associated with nocturnal activity were factors that in some way and over a long period of time made these various races nocturnal in habit. Now inherent in these forms of life, the propensity for nocturnal activity expresses itself when the stimuli of nocturnal factors recur in nightly rhythm. However, some animals show a recurring nocturnal-diurnal rhythm when they are kept in the laboratory under constant conditions of illumination, humidity and temperature (Welsh, '30b; Park and Keller, '32).

The most evident advantages of the nocturnal habit are:

1. *Avoidance of natural enemies active in daylight*

Thus, many spiders seek seclusion during the day, when they are the likely fare of reptiles and birds, and sought by many Hymenoptera. Millipedes and centipedes are eaten by various birds and reptiles. Mantids and walking-sticks are the food of lizards and birds, although they are seemingly protected in both color and form. Even roaches are eaten by daytime birds. Toads and frogs are eaten by hawks and snakes. Harvestmen, crickets, certain beetles, many moths, certain ants, various bats, rats and mice are other forms which may find activity at night a means of avoiding many daytime enemies.

There is greater safety at night for the uninterrupted feeding of herbivorous animals, such as fruitbats, capybaras, agoutis, rabbits, sloths, deer, moose and tapir. Animals engaged in feeding activities are apt to be especially vulnerable to their natural enemies.

2. *Easier acquirement of the preferred food at night*

This may be due to the invisibility of the hunter, the plentifulness at night of the intended prey, or the greater ease of detecting victims by the sense of smell. Odors remain longer in the air at night, due to greater humidity, and the relative absence of upward air currents. Further, if the prospective victims are themselves typically diurnal, they are more vulnerable at night on account of sleep or its equivalent, or their poorer adaptation for successful nocturnal activity. Such an advantage may be realized by carnivorous animals, including scorpions, spiders, tarantulas, centipedes, and among the vertebrates, alligators, boas, anacondas, pit-vipers, owls, most bats, raccoons and the various cats.

Scavengers and general feeders may be able to find food with more ease at night, due to better conditions for the use of the olfactory sense. Here might be listed the millipedes, roaches, many beetles, and the

vertebrate opossums, kinkajous, and armadillos.

3. Avoidance of excessive evaporation from the body

The atmosphere is at night as a rule cooler and damper than in the daytime. Animals that from the nature of their external covering would suffer from excessive evaporation through daytime activity, and would conceivably benefit from the nocturnal habit include earthworms, snails, *Peripatus*, cockroaches, mosquitoes, termites, toads and treefrogs. Thus Necheles ('27) reports that mosquitoes seem to prefer a relative humidity of 75 to 85 per cent, and that they retire during the day to avoid the excessive evaporating influence of daytime air with its low humidity and higher temperature.

4. Easier communication at night

Sounds produced have less competition, odors travel farther and are apparently stronger in the damp air. Photogenic organs are of value at night and useless by day. These advantages will be discussed under the heading "Usefulness of the several senses at night."

Some forms seem to benefit in two or three of these ways. In any one species, the reasons applicable can only be conjectured. Not all of the animals active at night can be seriously placed under any heading. Thus the fact that the long-horn grasshoppers are in some species nocturnal, in some diurnal, while practically all are apparently protectively colored and all face the same conditions, is difficult to explain. Along with almost any form active at night for any apparent reason, can be found a closely related form not active at night, yet exposed to the same conditions. The problem is hence a very complex one.

C. USEFULNESS OF THE SEVERAL SENSES AT NIGHT

When we seek to determine the adaptations exhibited by forms active at night, we encounter again much uncertainty. Such differences in sense organs as exist between nocturnal and diurnal forms of close relationship are differences of degree rather than of kind. There are a few definite adaptations in the way of light, sound and scent production. Nevertheless, with the possible exceptions of luminescence and some adaptations of vision, there is observed no modification which might not be fully as useful by day as by night. Our judgment is that the extreme development of some of these specializations of form and function is not so necessary by day as by night. The species described might be capable of successful nocturnal existence without any or all of the unusual modifications which they exhibit. The crucial point of development of each sense necessary for the successful nocturnal activity of each animal would be very difficult to determine, especially since the senses are not employed singly so often as collectively.

It would be difficult to tabulate in exactly certain order the relative usefulness of the various senses at night. The sense of smell is probably of greatest importance, and that of sight might be named last, but this arrangement would be questioned. It must be remembered that our ideas in regard to the sensations of animals other than ourselves, of invertebrates certainly, are only inferences from our own sensory experiences, and hence doubtless often inadequate and erroneous. We can never be sure that lower animals experience sensations in the same way that we do, even if the necessary receptor organs seem to exist.

1. The sense of smell

For purposes of communicating through this sense, it would be expected that the odors perceived by some individuals would be produced by others. Many such organs of scent production are known and there are undoubtedly many yet to be discovered. Numerous nocturnal animals have the necessary equipment. Harvestmen have scent glands near the anterior margin of the cephalothorax. In millipedes scent glands are present on various body segments. Walking-sticks have thoracic scent glands, used primarily for defense. The roaches have scent glands in certain abdominal segments, and give off a discernible fetid odor. Odor plays a very prominent part in the organization of termite colonies. In moths, glandular scales producing odor occur on the wings of various species, and at least in some groups the females possess a paired scent organ in the last abdominal segment. Army ants have a strong odor on which the organization of the colony depends heavily. The odor is produced by the pulvinate glands of the poison apparatus. Odors are also given off by the bugs and fireflies. Alligators produce musk from skin glands beneath the chin. Mammals yielding scent include the raccoon, skunk, porcupine, the cats, peccaries, muskrats, deer, elk, armadillos, and others. It will be noted that in addition to its usefulness in communication, scent production may be of value in defense, and in making the producing organism unpalatable to its enemies.

There is a wide variety of receptor mechanisms. Although spiders seem to have a well-developed sense of smell, the receptors apparently have not yet been located, unless certain hairs are olfactory in function, or the "lyriform organs" function in that capacity. However, Baerg ('28) indicates that tarantulas depend entirely on touch to locate food, seemingly placing no dependence on olfactory organs. In crickets the abdominal cerci are probably partly olfactory in function, as they are in roaches. Glaser ('27) shows that chemoreceptors are located also on the antennae of roaches, and that these are effective in detecting odors from a distance. In moths the antennae are probably chiefly olfactory in function and are more developed in the male (Mayer, '00). In Diptera, where the sense is well developed, work of Liebermann ('25) shows a rich supply of olfactory organs on the antennae. Olfactory organs may exist elsewhere than on the antennae. Indeed, McIndoo ('34) reports that in the blowfly the olfactory function is demonstrated by tarsi rather than antennae. Hymenoptera can detect delicate odors. Work of Hauser ('80), von Frisch ('21), Vogel ('23) and Wacker ('25) has designated the antennae as carrying olfactory organs in many species. McIndoo ('14 a, b, c; '16; '20) has reported the sense to be resident in other portions of the body as well. Some beetles (Valentine, '30) also have olfactory organs on the antennae. In other beetles the sense organs seem to be widely scattered over the body (Abbott ('27 a, b), McIndoo ('26)).

There are organs of other types which may be suspected of having an olfactory function, although this may be mixed with other sensations received from the same organs.

The well known nasal olfactory apparatus of the vertebrates needs no comment here.

Since the necessary equipment thus seems to exist in all of these groups, the olfactory sense may be suspected of functioning at night in at least four ways.

a. Congregating of individuals of the same species, and trail-following. Invertebrates

employing the sense for these purposes would include moths, termites and ants. In the last two groups named, the activity of the whole colony is doubtless directed chiefly by scent and odor. Some vertebrates that could be named in this connection are muskrats, beavers, raccoons, cats, porcupines, armadillos, bears and deer.

b. Sex attraction, by means of "alluring glands." Moths, beetles, roaches, walking-sticks and, among the vertebrates, alligators, deer, cats and peccaries would come in this category. The females of many moths and beetles, especially, emit an odor that attracts the males, often in considerable numbers. Sometimes the males also possess such glands.

c. Location of food. Animals in which this may be an important use of the sense are roaches, beetles, moths, mosquitoes, ants, armadillos, bears, porcupines, foxes, weasels, mice, rats, opossums, rabbits, raccoons and many others.

d. Detection of enemies and friends. This is apparently an important use of the sense in many vertebrate forms such as bears, deer, antelope and tapir, such invertebrate groups as the ants and termites, and doubtless many other insects.

2. *The sense of taste (closely associated with the olfactory sense)*

Among the invertebrates the organs of taste are difficult to demonstrate with certainty. Glaser ('27) reports chemoreceptors on the maxillary and labial palps of roaches. Minnich ('22a, '22b, '26a, '26b, '31) reports taste in the tarsi as well as the mouthparts of the butterfly and of the fly. In the honeybee, he ('32) reports contact chemoreceptors concerned with food choice in the antennae and first pair of legs as well as in the mouth parts. He concludes: "Taking bees, butterflies, and flies collectively, instances of contact chemoreceptors can be found in all or practically all of the head and thoracic appendages. It is suggested, therefore, that the ancestral insect may have possessed such receptors in each of its appendages." Probably the sense is very generally developed throughout the groups of non-aquatic invertebrates.

No special development of this sense would be expected in nocturnal animals beyond the conditions found among their daytime relatives. Perhaps our ideas on this point do not coincide with the actual situation, however, since the sense is so much more highly developed among many invertebrates than in ourselves, and hence probably much more significant in their lives than in ours. The occurrence of organs of taste in tarsal and antennal structures would seem to give the sense special usefulness at night for finding and inspecting food, if any species possessing such special equipment are active in the dark. Organs of taste certainly have large usefulness at night for inspecting food that cannot be seen.

Perhaps the only possible distinction between the senses of smell and taste is that if these end organs actually come in contact with the food they are considered gustatory; if they do not, they are considered olfactory. Both of these senses, when resident in antennal structures, are closely associated with that of touch, next to be discussed. There would thus be a contact-chemical sense of simple unified character.

Nocturnal arthropods which obviously have very delicate antennae on which they depend heavily for sensory experiences include centipedes, crickets, walking-sticks, roaches, termites, ants, moths, midges and mosquitoes. They are doubtless just as important in other insects whose antennal equipment is not so apparently depended upon.

3. The sense of touch

Organs of touch are of value at night in moving about, in inspecting food or other objects encountered, and in perceiving vibrations, this last faculty passing into that of hearing, which will be considered separately. Among the invertebrates many sensitive and elaborate devices for stimulating end organs are found. Delicate tactile hairs are distributed over the body and appendages in many species. The antennae have already received comment.

In the vertebrates, aside from the general sensitivity of the skin, we find such special developments as the vibrissae of rodents and various other mammals, the delicate muzzle of the deer, and the very sensitive organs of the nose and wings of the bat. Lynn ('30) reports that the facial pits of the pit-vipers function in the perception of air vibrations. The pit membrane is a modification of the integument of the head. All of these organs are devices for stimulating nerve terminations.

4. The thermal sense

Closely associated with the tactile sense is sensitivity to temperature. Wheeler ('26) notes concerning ants, "that these insects have a delicate temperature sense, although the location and nature of its organs are quite unknown, is shown by many of their habits, notably by the way they regulate their hours of activity. . . ." Temperature, correlated of course with humidity and air movements, doubtless affects the degree of activity of many animal forms. Kennedy ('27) notes that insects, with a large surface-to-volume ratio and coldblooded nature, have a special problem with reference to temperature changes.

5. The sense of hearing and sound production

The sense of hearing is closely allied to that of touch. Sound production and reception is an important means of communication between members of the same species at night, as well as by day, and is important in the detection of approaching enemies or victims, as the case may be. Sound-making serves to frighten away enemies, to warn others of their approach, to attract and woo mates, to communicate general information. Noble ('31) says that "the chief function of the voices of frogs and toads is to attract mates," but lists other possible uses of the voice. Vertebrates apparently depending at least in part on this sense for communication at night include alligators, some geckoes, owls, goat-suckers, shrews, bats, mice, cats, foxes, coyotes, rabbits and hares, howler-monkeys, and many others.

Among invertebrates (both nocturnal and diurnal), sound is produced by stridulating organs or other sound-making devices, through the use of vibratory structures of various types, or the tapping of surrounding objects.

Many spiders have stridulating organs, but the stridulation is not always audible to human ears. These organs occur variously on the mouthparts, or thorax and abdomen. Since no certain auditory apparatus has been discovered in the spiders, it is probable that these stridulatory organs are for giving warning signals to other animals, not for use as means of communication with other spiders. Indirect evidence that spiders can hear is, however, presented by the fact that in certain groups, the males alone have stridulatory organs. Unless the females have auditory powers, this fact is difficult to explain.

Among wood-boring beetles, ticking or clicking serves as a means of communication, and doubtless helps to keep the colony together. Thus *Passalus* beetles have stridulatory organs on the abdomens of adults, on the middle legs of larvae. In

the "death-watch" beetles such ticking is believed to function in attraction of the opposite sex. The tegmina of male "grass hoppers" are furnished with stridulating organs. Auditory tympana are present in the fore tibiae. Male crickets stridulate by means of a file and scraper arrangement on the wings. Crickets have tympana on the fore tibiae, except in a mute wingless species. Mole crickets have tympana in the fore tibiae. The males can produce a dull jarring note. Among crickets and grasshoppers, the females are attracted to the males by their chirping. The synchronous chirping of two or more males seems to show that sound is heard by them as well as by the females. Allard ('28) points out that the stridulation of Orthoptera possesses tonality in the case of the crickets, highly specialized technique and variety among the katydids, and rhythm in both of these groups. Vibration of wing elements is the stridulating device most frequently observed in Orthoptera.

Some moths apparently possess stridulating organs. Wing vibration may function as a means of attracting the opposite sex, but according to the Raus ('29) this assists in the dissemination of the odor which is known to be an effective agent. The vibration may not be attractive in itself.

In mosquitoes the humming of the wings is a means of communication. Some of the delicate fibrillae of the bushy antennae of the male vibrate sympathetically with the wing note of the female. Child ('94) describes an experiment conducted with the aid of a tuning fork and concludes that the vibration of the fibrillae acts upon a complex organ found in the second basal segment of the antenna. As this organ functions only when the hairs are at the proper angle to the sound waves, the male mosquito can perceive not only the sound but also the direction of it. Buzzing is a means by which female flies attract males.

Some bees doubtless influence others by buzzing. Among ants chordotonal organs may occur in the tibiae of all pairs of legs, at the bases of the antennae, and elsewhere on the body. Ants exhibit varying stridulatory powers.

It must be remembered that many sounds that we cannot hear, because of their being too high or too low in pitch, are produced and heard by other animals. This is especially true of the insects. Further, the kind of sound to which the human mind adjusts itself evidently differs from that which is most significant to the animal. Man is rather little concerned with the sounds and noises which the things themselves produce and which are meaningful for the animal. The sounds which most often concern man are those of organized speech which merely refer to the objects.

6. Light production and the sense of sight

Among arthropods light is produced by fireflies of both sexes and the larvae, the elaters and their larvae, and by numerous other forms (Harvey, '20). The photogenic organs of lampyrids consist of granular cells enclosed in a network of fine tracheae. These cells have the power of secreting a substance which is luminous when acted upon by oxygen from the tracheae in the presence of moisture. Fundamentally, this effect seems to depend upon a luciferin-luciferase reaction (Harvey, '20, '32), although not all luminous animals give the reaction (Harvey, '26). There are various luciferins and luciferases, specific for the forms exhibiting them. These are similar in closely related luminous species, relatively unlike in more distantly related forms. There is a reflecting layer of cells beneath the photogenic cells. The reflecting medium is a white urate,

secreted by the cells of this deeper layer. The mass of branching tracheae makes possible the rapid oxygenation and the resulting flash of the fireflies. Allard ('31) notes that the rate of flashing may be modified by temperature. Light so produced ranges among various animals from green to various shades of red, purple and violet. Several colors may be emitted by different organs on the same animal. Snell ('31), working on *Photuris pennsylvanica*, concluded

> that the mechanism controlling the flashing is responsive to nervous and to direct electrical stimulation, that it effects the control by regulating the admission of oxygen to the cells containing the photogenic substances, and that variation in the character of the flash is brought about by variation either of the number of units stimulated or of the amount of stimulation and response (admission of oxygen to the cells) in the unit involved. The tracheal end cell, which has for a long time been considered by histological investigators to be responsible for the control of luminescence, is certainly the responsive mechanism in this control.

There are many gradations in complexity of light organs among various animal species.

Light production has sometimes been considered as simply a by-product of metabolism, but the phenomenon that has been often observed (recently, Morrison, '29; Howard, '29; Merrill, '30; Richmond, '30; Rau, '32) of the synchronous flashing of the fireflies in a given area, would seemingly indicate that the light produced by one is perceived by other individuals, and that they are influenced by it. (However, Rau interprets this as being originally a simultaneous response of individuals to a sudden environmental change, followed by accidental flashing in unison until they "break step.") The flashing of fireflies has also been observed to have a part in sex attraction (McDermott, '12; Mast, '12). The luminous "eyes" of adult elaters are thought by some to be of "horrifying" or warning intent. Harvey ('20) writes that some animals possess a periodicity of luminescence. They only luminesce at night and are difficult to stimulate during the day. Further, these animals are negatively heliotropic to a very strong extent, and lie hidden during daylight.

The opportunity for the employment of the sense of sight at night is quite limited compared to its daytime importance. However, some animals can apparently see quite well, even when there is no moon. That eyes are subject to adaptation is eloquently testified by the fact that cave animals have degenerate eyes or are eyeless.

Concerning visual cells in general, it is evident that eyes may perform three functions, to determine the intensity of light, to perceive the direction of illumination, or to record light-images of the objects from which the rays come. Some eyes have all three functions. The body surface of some animals contains other light-sensitive cells than those in the eyes, and these can perceive light and even its direction. If deprived of its eyes, a frog can still orient itself to a light beam. Such perceptive cells are also possessed by the earthworm, and by the crayfish. In this discussion we shall disregard the possible occurrence in the forms studied of light-sensitive cells other than those in eyes, and shall speak only of visual cells that are grouped into eye structures.

The types of eyes to be considered are:

a. Ocelli, or similar structures, of invertebrates. Beneath a simple polished lens is a vitreous body and retina, along with nerve fibers, pigmented hypodermis cells and accessory cells. A reflecting tapetum may or may not back up the ocellus. When present it supposedly assists in nocturnal vision or at least in light perception.

Both ocelli and compound eyes are present usually, but the ocelli may be

totally absent, as in beetles; compound eyes may be lacking, as in spiders, millipedes, centipedes, Collembola; or both sorts of eyes may be practically absent, as in some ants and termites except winged reproductive individuals. There are many variations of each type of eye.

b. Compound eyes, of invertebrates. Beneath each of the many facets in arthropod eyes is an ommatidium, consisting besides the cornea of lens, rhabdome and retinula, pigment, both distal (iris) and proximal (retinal), sometimes accessory (tapetal) pigment cells, a basement membrane, and fibers of the optic nerve. In bright light the pigment cells elongate around the ommatidium and absorb the excess of light. In dim light they shorten, absorbing a minimum amount of light, and permitting a maximum amount of it to reach the rhabdomes. On account of the withdrawal of pigment the image formed by night-eyes is probably superimposed to some extent, being reinforced by adjacent ommatidia; that of day-eyes is mosaic. Some eyes are fixed as day-eyes, with much pigment; some as night-eyes, with little pigment; some are capable of the adjustment described.

Welsh ('30a, b) describes a very definite migration of distal pigment in eyes of certain shrimps. In another study ('32) he writes that the tapetal or reflecting pigment of crustacean eyes consists of amorphous guanin which forms a layer behind the image receptors, thus increasing eye efficiency at low light intensity. This remarkably effective reflecting pigment moves under the influence of light and dark and is especially motile in certain tropical fresh-water crustaceans which are mainly nocturnal. The nature of the movement of guanin particles seems to approximate the movement of melanin in melanophores, with an additional movement amoeboid in character. In two Cuban species the distal pigment cells of the eye show a daily rhythmical movement even under constant illumination. He believes the movement to be controlled directly by the blood, indirectly by the nervous system. The reflecting and retinular pigment fails to show this rhythm, thus indicating that the two sets of pigment are independently controlled. Ordinarily the proximal retinular pigment streams distally in the light, proximally in darkness. Bennitt ('32) also observed rhythmical activity of the proximal pigment cells of the crayfish, in the absence of the usual stimuli promoting such changes. He ascribes this rhythm to a metabolic periodicity acting through the circulation, and roughly correlated with the periods of light and darkness to which the animal is subjected in nature. In another paper he and Merrick ('32) present evidence that distal migration, of proximal pigment, while influenced primarily by light, may be induced by agents such as low temperature and carbon dioxide, which reduce the metabolic rate of the animal.

Sharp ('18) describes the divided compound eyes of mayflies as having two parts; one of which is a day-eye, and the other a night-eye, with the two parts widely separated so that the insect appears to have two pairs of compound eyes. The portion of the eye that functions as a day-eye is composed of much smaller facets and the pigment mechanism is that characteristic of day-eyes. The part of the eye that functions at night is composed of larger facets and is fitted to produce a superimposed image.

Hanstrom ('27) believes that in insect eyes the shorter retinal cells may be compared with the rods, the longer ones with the cones of vertebrates.

c. Vertebrate eyes. The well-known vertebrate eye needs no description. There are various devices for adapting such eyes

to the amount of light received, either temporarily or habitually.

The phenomenon of pigment migration in cells of the epithelial layer of the retina occurs quite commonly. As Laurens and Detwiler ('21) explain in the case of the alligator eye, in twilight vision, when the rods alone are capable of being stimulated to any degree, or in complete darkness, the pigment moves back and leaves the spaces between the rods free. Owing to refraction and diffusion, the effect of dim light is greater than if the rods are covered by pigment, when the light can only pass along the axis of the rod. The cones in twilight vision are not functional, on account of their high threshold. They elongate and move out of the way. The rods contract, coming into their best position.

In bright light, the pigment migrates and protects the rods, which have a low threshold, and are made particularly sensitive by the accumulation of visual purple in the dark. The rods elongate, the less sensitive cones are drawn out of the pigment by contraction of the myoids, and are thereby made accessible to stronger light stimulus.

Walls ('28) writes:

> If the photomechanical changes in the retina be considered from a comparative standpoint, their story is one of degeneration. In the fishes the phenomena are rapid and pronounced; in the amphibians they are less rapid and in general less marked, though still obviously of functional value; in the reptiles only long exposures have resulted in measurable differences in pigment and cone positions in light and darkness. In the mammals, the phenomena seem to have practically disappeared.

Nocturnal animals generally show a preponderance of retinal rods, while diurnal species often possess more cones than rods. Rods, the mechanism of vision in dim light (of brightness, not of color) are the only visual cells found in the eyes of some nocturnal geckoes and bats. Cones, which function in both brightness vision and color reception, are apparently the only visual cells in the eyes of some diurnal lizards. Most turtles and many snakes probably have only cones. Other forms such as crocodiles and their relatives and some snakes possess both rods and cones. Walls ('32b) after finding visual purple in the eyes of many snakes, states that "rods are to be expected, either to the exclusion of cones or in combination with them, in all Boidae, in all Viperidae, and in such Colubridae as have vertical pupils." According to Slonaker ('18) there is a preponderance of color-perceiving cones in the sparrow (diurnal) retina. Woollard ('27) distinguishes between nocturnal and diurnal primates on the basis of retinal structure, the diurnal species having a dominance of cones over rods, especially in the fovea. Cones are normally absent in the mouse (Keeler, '28; Moody, '29). Verrier ('32) reports retinas that seem to contradict this Duplicity Theory. The classic definitions of rods and cones are subject to some revision. It is possible that a re-examination of the visual cells in the retinas which she reports to be exceptions may bring them into harmony.

There are other kinds of adaptation. Movements of the iris regulate the amount of light reaching the retina. Reduction of pupil size protects the retina from strong light. Dilation makes all possible illumination available in dim light. In many amphibia the iris is capable of moderate contraction or expansion. Extensive movement may occur in many reptiles, and a vertically elliptical pupil characterizes the eyes of numerous nocturnal species. Walls ('32a) explains that "a vertically elliptical pupil is capable of more complete closure than is a round pupil. . . . The pure-cone reptilian eye not being subject to dazzle at ordinary

intensities is served quite well by a round pupil, while a rod-and-cone eye such as that of the rattlesnake must have an elliptical pupil. The pure-rod eye sometimes has a pupil which is capable of absolute closure, as in many geckoes." He also notes that all mammals which have vertical pupils are nocturnal, although most nocturnal mammals have round pupils. Kolmer ('26) reports for bats an especially developed sphincter muscle in the iris. Most nocturnal birds have large eyes with pupils capable of exceptional dilation. Walls ('28) considers the forward evolution of the iris reaction, culminating in the very rapid and extensive response found in the mammals, to be correlated with the backward orthogenesis of photomechanical changes, as noted above. He observes "Certainly the rapid pupil reaction, measured in seconds, is a decided improvement over the sluggish pigment and cell movements whose minimum reaction time at best, in certain fishes, is many minutes."

Walls ('31) also indicates that we may expect to find colorless lenses in the eyes of nocturnal snakes, for reasons opposite to those that have brought about yellowness of lens (promoting visual acuity) in several diurnal species investigated by him. He writes that "Snakes with vertical pupils and nocturnal habits would have no need of yellow lenses, in fact such would be absolutely detrimental to a nocturnal snake since they would decrease the already low intensity of the available illumination." This principle holds true in other animal groups. Walls and Judd ('33) observe that typical nocturnal vertebrates also have clear corneae and colorless droplets in the retinal cones. (Rods possess no droplets.) Usually there are neither colored maculae nor plexuses. That is, nocturnal vertebrates usually lack the yellow and red intraocular filters found in one or another of these forms in most sun-loving species.

In nocturnal mammals Kahmann ('30) observes that the eye and lens are relatively large, the lens strongly curved and highly refractive. He reports that in Ungulates, Carnivores and Primates the ciliary muscle is well developed and accommodation is better than in other forms examined, but he believes that in general there is little accommodation in the eyes of nocturnal lower mammals, due to the size and hardness of the lens.

The presence of a tapetum is an almost absolute criterion of a nocturnal animal. This structure behind the retina reflects back the light entering the eye, causing the well-known shining of eyes in the dark. This may be observed in the eyes of cats, opossums, kinkajous, alligators, etc. It is believed that reflection increases the effect of a faint light, by causing it to pass through the retina a second time. In structure the tapetum varies among different groups. In alligators it consists of whitish guanin granules included in cells of the pigment epithelium. The "*tapetum lucidum*," choroidal reflecting structure in the eyes of carnivores, ruminants and perissodactyls, consists of fibrous tissue. The colors of glow observed in tapetal reflections are probably due to surface colors and interference phenomena.

SUMMARY

1. Absence of light is the most characteristic factor of the nocturnal environment, for vertebrates at least. Many animals appear to be attuned to a certain range of intensity of light. The degree of activity of nocturnal animals may be modified by this and other factors, such as temperature, humidity and rate of evaporation. Nocturnal rhythms, once established, may be exhibited even when the animals are kept

under constant conditions of illumination, humidity and temperature.

2. Possible advantages of the nocturnal habit include the avoiding of daytime enemies, easier obtaining of preferred food, avoidance of excessive evaporation from the body, and easier communication between individuals. For any one species, the reasons applicable can only be conjectured.

3. The adaptations to nocturnal life are chiefly the unusual refinements of one or more of the senses. These are differences of degree rather than of kind and are difficult to analyze, especially since the senses are not employed singly so often as collectively. With the possible exceptions of luminescence and some adaptations of vision, there is observed no modification that might not be fully as useful by day as by night.

4. The closely related senses of smell and taste (and general chemical sense) are relatively the most important for nocturnal use. The sense of smell, frequently aided by organs of scent production, assists in the congregating of individuals, in following trails, in sex attraction, in locating food, and in the detection of enemies and friends. The sense of taste has special usefulness at night for inspecting food which cannot be seen.

5. The sense of touch is of value at night in moving about, in inspecting food or other objects encountered, and in perceiving vibrations, this last faculty passing into that of hearing.

6. The thermal sense plays a part in regulating the time and intensity of activity, especially among insects.

7. The sense of hearing, often correlated with sound production, is important in the detection of approaching enemies or victims, and for communication. Sound-making on the part of animals serves to frighten away enemies, to warn others of their approach, to attract and woo mates, to communicate general information.

8. Eyes present more definite anatomical adaptations for nocturnal life than any other sense organs. Light production probably has some part in sex attraction and congregating, and may serve as a warning signal.

9. The adaptations for nocturnal vision found among invertebrates include the division of the eye into two parts, each with characteristic structure and one of which is for nocturnal vision; pigment migration; and the presence of a reflecting tapetum.

10. Keenness of vision at night among the vertebrates depends anatomically on the possession of a rod-rich retina, on pigment withdrawal and rod shortening, and often on the presence of a light-reflecting tapetum, by means of which the rods are doubly stimulated. These processes may be accompanied or (especially in mammals) even largely replaced by accumulation of visual purple and related substances, and by iris dilation. Frequently the iris has a vertical aperture. Typical nocturnal vertebrates lack the yellow or red intraocular filters characteristic of nocturnal forms. They also tend to have relatively large eyes. Other possibly useful adaptations are mentioned.

LIST OF LITERATURE

ABBOTT, C. E. 1917a. Experimental data on the olfactory sense of Coleoptera, with special reference to the Necrophori. *Ann. Ent. Soc. America*, Vol. 20: pp. 207–216.

———. 1917b. Further observations on the olfactory powers of the Necrophori. *Ann. Ent. Soc. America*, Vol. 20: pp. 550–553.

ALLARD, H. A. 1918. Remarkable musical technique of the larger angular-winged katydid. *Science*, Vol. 67: pp. 613–14.

ALLARD, H. A. 1931. The photoperiodism of the firefly *Photinus pyralis* Linn: Its relation to the evening twilight and other conditions. *Proc. Ent. Soc. Wash.*, Vol. 33: pp. 49–58.

BARRO, W. J. 1928. The life cycle and mating habits of the male tarantula. QUART. REV. BIOL., Vol. 3: pp. 109–116.

BENNITT, RUDOLPH. 1932. Diurnal rhythm in the proximal pigment cells of the crayfish retina. *Physiol. Zool.*, Vol. 5: pp. 65–69.

BENNITT, RUDOLPH, and A. D. MERRICK. 1932. Migration of the proximal retinal pigment in the crayfish in relation to oxygen deficiency. *Biol. Bull.*, Vol. 62: pp. 168–177.

CHILD, C. M. 1894. Ein bisher wenig beachtetes antennales Sinnesorgan der Insecten, mit besonderer Berücksichtigung der Culiciden und Chironomiden. *Zeits. wiss. Zool.*, Vol. 58: pp. 478–528.

CRAWFORD, STANTON C. 1931. Nocturnal adaptations. *Proc. Pa. Acad. Sci.*, Vol. 5: pp. 54–61.

———. 1932. Twilight and dawn in Guiana. *Natural History*, Vol. 32: pp. 207–214.

———. 1933. A survey of nocturnal vertebrates in the Kartabo Region of British Guiana. *Journ. An. Ecol.*, Vol. 2: pp. 282–288.

FRISCH, KARL v. 1911. Über den Sitz des Geruchsinnes bei Insecten. *Zool. Jahrb., Abt. f. allgem. Zool. u. Physiol.*, Vol. 38: pp. 449–516.

GLASER, R. W. 1927. Evidence in support of the olfactory function of the antennae of insects. *Psyche (Boston)*, Vol. 34: pp. 209–215.

HANSTROM, B. 1927. Über die Frage ob funktionell verschiedene, zapfen-und stäbchenartige Sehzellen im Komplexauge der Arthropoden vorkommen. *Zeitschr. Wiss. Biol., Abt. C., Zeitschr. Vergleich. Physiol.*, Vol. 6: pp. 566–597.

HARVEY, E. N. 1910. The Nature of Animal Light. J. B. Lippincott Co. *Phila.*

———. 1916. Additional data on the specificity of luciferin and luciferase, together with a general survey of this reaction. *Amer. Jour. Physiol.*, Vol. 77: pp. 548–554.

———. 1932. The evolution of bioluminescence and its relation to cell respiration. *Proc. Amer. Phil. Soc.* Vol. 71: pp. 135-141.

HAUSER, G. 1880. Physiologische und histologische Untersuchungen über das Geruchsorgan der Insekten. *Zeitschr. Wiss. Zool.*, Vol. 34: pp. 367–403.

HOWARD, S. F. 1929. Synchronous flashing of fireflies. *Science*, Vol. 70: p. 556.

KAHMANN, HERMANN. 1930. Untersuchungen über die Linse, die Zonula ciliaris, Refraktion und Akkommodation von Saügetieren. *Zool. Jahrb., Abt. Allg. Zool. u. Physiol. Tiere*, Vol. 48: pp. 509–588.

KEELER, CLYDE E. 1928. Blind mice. *Jour. Exp. Zool.*, Vol. 51: pp. 495–508.

KENNEDY, C. H. 1917. Some non-nervous factors that condition the sensitivity of insects to moisture, temperature, light and odors. *Ann. Ent. Soc. America*, Vol. 10: pp. 87–106.

KOLMER, WALTER. 1926. Über die Augen der Fledermäuse. *Verhandl. Zool.—Bot. Ges. Wien*, Vol. 74/75 (1924–1925).

LAURENS, H., and DETWILER, S. R. 1921. Studies on the retina. The retina of *Alligator mississippiensis* and its photomechanical changes. *Jour. Exp. Zool.*, Vol. 32: pp. 207–234.

LIEBERMANN, A. 1925. Correlation zwischen den antennalen Geruchsorganen und der Biologie der Musciden. *Zeitschr. f. Morph. u. Ökol. d. Tiere*, Vol. 5: pp. 1–97.

LYNN, W. GARDNER. 1930. The structure and function of the facial pit in the pit vipers. *Anat. Rec.*, Vol. 47: pp. 353–354.

MAST, S. O. 1912. Behavior of fireflies (*Photinus pyralis*) with special reference to the problem of orientation. *Jour. An. Behav.*, Vol. 2: pp. 256–272.

MAYER, A. G. 1900. On the mating instinct in moths. *Ann. and Mag. Nat. Hist.*, Series 7 (5): pp. 183–190.

McDERMOTT, F. A. 1912. Recent advances in our knowledge of the production of light in living organisms. *Rept. Smithson. Inst.*, 1911, pp. 345–362.

McINDOO, N. E. 1914a. The olfactory sense of the honey bee. *Journ. Exp. Zool.*, Vol. 16: pp. 265–346.

———. 1914b. The olfactory sense of insects. *Smithson. Misc. Coll.*, Vol. 63: pp. 1–63.

———. 1914c. The olfactory sense of Hymenoptera. *Proc. Phila. Acad. Nat. Sci.*, Vol. 66: pp. 294–341.

———. 1916. The sense organs on the mouth parts of the honey bee. *Smithson. Misc. Coll.*, Vol. 65: pp. 1–55.

———. 1920. The senses of insects. *Ann. Rept. Smithson. Inst.*, pp. 461–483.

———. 1926. Senses of the cotton boll weevil—an attempt to explain how plants attract insects by smell. *Journ. Ag. Research.*, Vol. 33: pp. 1095–1141.

———. 1934. Chemoreceptors of Blowflies. *Jour. Morph.*

MERRILL, R. H. 1930. Synchronous flashing of fireflies. *Science*, Vol. 71: p. 132.

MINNICH, D. E. 1922a. The chemical sensitivity of the tarsi of the red admiral butterfly, *Pyrameis atalanta* Linn. *Jour. Exp. Zool.*, Vol. 35: pp. 57–81.

———. 1922b. A quantitative study of tarsal sensitivity to solutions of saccharose, in the red admiral butterfly, *Pyrameis atalanta* Linn. *Jour. Exp. Zool.*, Vol. 36: pp. 445–457.

———. 1926a. The chemical sensitivity of the tarsi of certain muscid flies. *Biol. Bull.*, Vol. 51: pp. 166–178.

———. 1926b. The organs of taste on the proboscis of the blowfly, *Phormia regina* Meigen. *Anat. Record*, Vol. 34: p. 126.

———. 1931. The sensitivity of the oral lobe of the proboscis of the blowfly, *Calliphora vomitoria* Linn. to various sugars. *Journ. Exp. Zool.*, Vol. 60: pp. 121–139.

———. 1932. The contact chemoreceptors of the honey bee, *Apis mellifera* Linn. *Journ. Exp. Zool.*, Vol. 61: pp. 375–393.

MOODY, PAUL A. 1929. Brightness vision in the deer-mouse *Peromyscus maniculatus gracilis*. *Journ. Exp. Zool.*, Vol. 52: pp. 367–406.

MORRISON, T. F. 1929. Observations on the synchronous flashing of fireflies in Siam. *Science*, Vol. 69: pp. 400–401.

NECHELES, HEINRICH. 1927. Observations on the causes of night activity in some insects. *Chinese Jour. Physiol.*, Vol. 1: pp. 143–155.

NOBLE, G. K. 1931. The Biology of the Amphibia. McGraw Hill Book Co. *N. Y.*

———. 1934. The structure of the facial pit of the pit vipers and its probable function. *Anat. Rec.*, Vol. 58: Suppl. p. 4.

PARK, ORLANDO, JOHN A. LOCKETT and DWIGHT J. MYERS. 1931. Studies in nocturnal ecology with special reference to climax forests. *Ecology*, Vol. 12: pp. 709–727.

PARK, ORLANDO, and JOHN G. KELLER. 1932. Preliminary analysis of activity rhythm in nocturnal forest insects. *Ecology*, Vol. 13: pp. 335–346.

RAU, P. and N. 1929. The sex attraction and rhythmic periodicity in giant saturniid moths. *Trans. Acad. Sci. St. Louis*, Vol. 26: pp. 81–221.

RAU, PHIL. 1932. Rhythmic periodicity and synchronous flashing in the firefly *Photinus pyralis* with notes on *Photuris pennsylvanica*. *Ecology*, Vol. 13: pp. 7–11.

RICHMOND, C. A. 1930. Fireflies flashing in unison. *Science*, Vol. 71: pp. 537–538.

SHARP, D. 1918. Insects. Article in Cambridge Natural History.

SLONAKER, J. R. 1918. A physiological study of the anatomy of the eye and its accessory parts of the English sparrow (*Passer domesticus*). *Jour. Morph.*, Vol. 31: pp. 351–460.

SNELL, PETER A. 1931. The neuro-muscular mechanism controlling flashing in the lampyrid fireflies. *Science*, Vol. 73: pp. 372–373.

VALENTINE, J. M. 1930. The olfactory sense of the adult meal-worm beetle, *Tenebrio molitor* (Linn.). *Jour. Exp. Zool.*, Vol. 58: pp. 165–227.

VERRIER, MLLE. M. L. 1932. Physiologie comparée des cônes et des bâtonnets. Indications fournies par l'étude du comportement. *Comp. Rend. Acad. Sci. (Paris)* Vol. 195: pp. 1333–1335.

VOGEL, R. 1923. Zur Kenntnis des feineren Baues der Geruchsorgane der Wespen und Bienen. *Zeitschr. f. Wiss. Zool.*, Vol. 120: pp. 281–324.

WACKER, F. 1925. Beiträge zur Kenntnis der antennalen Sinnesorgane der Hymenopteren, *Zeitschr. Morph. u. Ökol. d. Tiere*, Vol. 4: pp. 739–812.

WALLS, GORDON L. 1928. The photo-mechanical changes in the retina of mammals. *Science*, Vol. 67: pp. 655–656.

———. 1931. The occurrence of colored lenses in the eyes of snakes and squirrels and their probable significance. *Copeia*, 1931 (3): pp. 125–127.

———. 1932a. Pupil shapes in reptilian eyes. *Bull., Antivenin Inst.* Vol. 5: pp. 68–70.

———. 1932b. Visual purple in snakes. *Science*, Vol. 75: pp. 467–468.

Walls, Gordon L. and H. D. Judd 1933. The intraocular colour-filters of vertebrates. *Brit. Journ. Ophthalmol.*, Vol. 17: pp. 641–675, 705–725.

WELSH, JOHN H. 1930a. The mechanics of migration of the distal pigment cells in the eyes of Palaemonetes. *Jour. Exp. Zool.*, Vol. 56: pp. 459–494.

———. 1930b. Diurnal rhythm of the distal pigment cells in the eyes of certain crustaceans. *Proc. Nat. Acad. Sci.*, Vol. 16: pp. 386–395.

———. 1932. The nature and movement of the reflecting pigment in the eyes of crustaceans. *Jour. Exp. Zool.*, Vol. 62: pp. 173–183.

WHEELER, W. M. 1926. Ants. Columbia University Press. *New York.*

WOOLLARD, H. H. 1927. The differentiation of the retina in Primates. *Proc. Zool. Soc. London*, (1): pp. 1–17.

HYPERPARASITISM IN PROTOZOA

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THE PARASITES OF PROTOZOA

THE interrelations among organisms in nature are wonderfully diverse. Symbiosis—the association of organisms for their mutual advantage; and parasitism—the existence of one organism at the expense of another—are two opposite extremes of the same phenomenon.

Parasitism has attracted much attention. Among plants and animals parasites are very numerous. Only two phyla of animals, Echinodermata and Tunicata, contain no parasitic forms. Some classes of animals, such as the Sporozoa, Trematoda, Cestoda, and Acanthocephala, are exclusively parasitic. On the other hand, all animals and plants may serve as hosts for these parasites. The parasites themselves form no exception in this respect, and may be invaded by other parasitic forms. This phenomenon is known as hyperparasitism. The hyperparasites in their turn are not free from invasion by other parasites. Instances of triple and quadruple parasitism are known.

Parasites of Protozoa have been recognized for many years. Judging from their illustrations Müller (1856), Carter (1856–1857), Wallich (1863), Greef (1866), and other authors have presented descriptions of parasites in Rhizopoda, Mastigophora and Infusoria. Parasitic Protozoa may be parasitized by bacteria, fungi, worms, and other species of Protozoa. The parasite passes into a protozoon through its mouth opening, like any food particle, a food vacuole being formed round it. As shown by recent investigations, the reaction of a food vacuole is at first either acid or alkaline. The rôle of the acid in the food vacuole is not fully understood. It is supposed that the ingested organisms are killed by it.

Not all of the ingested organisms are killed during the acid phase; some are able to survive unharmed, even finding this environment favorable for multiplication and development. Such a condition is seen among amoebae, when the bacteria they ingest become pathogenic for them. Nägler (1910) has described the invasion of an amoeba (*Amoeba limax* in type) by cocci. I have had an opportunity of observing the same amoeba, in plate-culture, invaded also by cocci. The latter multiplied within the cytoplasm of the amoebae, formed large clumps, and at last brought about the death of their hosts.

BACTERIAL PARASITES

The bacterial infection of free-living Protozoa has been studied rather fully by Petschenko in the case of *Paramoecium caudatum*. This author revealed the occurrence of bacteria (*Drepanospira mülleri*) not only in the cytoplasm, but in the nucleus as well. In both cases the bacteria multiplied profusely, occupied a considerable volume in the body of the ciliate, and finally caused the death of the host.

The portal by which bacteria gain entrance to the body of the host may be not only the mouth opening, but the whole body surface of a protozoon. *Opalina ranarum*, a ciliate parasitic in the intestine

of certain Amphibia, lacks a mouth opening, the food material passing into the body through the surrounding pellicle by osmosis. When studying the cytoplasmic inclusions in *Opalina* (1922–1923), I had the opportunity of observing in the cytoplasm of some individuals a large number of bacteria gathered in clusters. It seemed probable that the bacteria penetrated the damaged pellicle, but it is also possible that bacteria might pass through the intact membrane, when under the influence of certain external factors chemical changes take place in it.

PARASITISM DUE TO FUNGI

Protozoa are most frequently attacked by Chytridia, fungi which have been known for many years to occur in them. The first observations were made on free-living protozoa. Dangeard (1895) found these fungi within the nucleus of *Amoeba verrucosa*, and named them *Nucleophaga amoebae*. During development and formation of zooconidia the nucleus of the amoeba degenerated and the amoeba itself succumbed. Gruber (1904) noted similar parasites in *Amoeba viridis;* Penard (1905) in *Amoeba terricola*, Doflein (1907) in *Amoeba vespertilio*, Mercier (1907–1910) in *Endamoeba blattae*.

In parasitic Protozoa, Chytridia attack either the cytoplasm or the nucleus. At the present time these fungi are known in parasitic Amoebae, Mastigophora and Ciliata.

Leger and Duboscq (1904) found the cytoplasmic parasite *Sphaerita* in *Endamoeba salpae*, parasitic in the rectum of the marine fish, *Box salpa* and *B. boops*. Wenyon (1907) observed similar parasites in *Endamoeba muris* from the intestines of mice. Mackinnon (1913–1914) describes cocci-shaped parasites in *Endamoeba minchini* from the intestine of *Tipula* (sp.) larvae. I observed (Sassuchin, 1929) cytoplasmic parasites in *Mastigina hylae* from the intestines of tadpoles of *Rana*.

Cytoplasmic parasites are known also in the intestinal amoebae of man, such as *Endamoeba coli* (Cragg, 1919; Nöller, 1921; Epstein, 1922; Lwow, 1925), *Endamoeba histolytica* (Nöller, 1921; Lwow, 1925), *Endolimax nana* (Dobell, 1919), *Iodamoeba bütschlii* and *Dientamoeba fragilis* (Nöller, 1921).

As a rule these parasites occur as rounded bodies within the cytoplasm of the amoebae. Such bodies, measuring 1 to 2.5 microns in diameter, are scattered in the protoplasm either singly or more frequently united into groups sometimes closely resembling sporangia, except for the absence of a membrane. Such groups may occupy three fourths of the protoplasm of the host; moreover, there are not infrequently several groups in one amoeba. As a direct consequence of such invasion the parasitized amoebae die. By the rupture of their bodies the parasites escape into the lumen of the intestinal canal and here they may invade other amoebae. Parasites were found by us in the intestinal amoebae of monkeys (*Macacus rhesus*) (Sassuchin, Popow, Kudrjawzew and Bogenko, 1930). In the protoplasm of *Endamoeba pitheci*, rounded clumps of bodies enclosed in a vacuole were revealed. In their form, structure, and position they were identical with the parasites that occur in the intestinal amoebae of man. Occupying a considerable part of the body of the amoeba (see fig. 1) they destroyed its protoplasm and the amoeba succumbed. It is to be noted that in the intestinal amoebae of monkeys the parasites are of rare occurrence. Quite a different picture was observed in the intestinal amoebae of a steppe suslik (*Citellus pygmaeus* Pallas). Parasites occurred in large numbers in *Endamoeba citelli*. In certain microscopic fields all the amoebae were invaded by these fungi (fig. 2). Within the cytoplasm of their host, the parasites are collected in groups of separate

bodies, each group looking something like a sporangium. These bodies are never to be seen enclosed in one membrane, but one or several groups of such bodies are present in the cytoplasm of an amoeba. These groups vary considerably in size, at times being quite as large as the nucleus of the amoeba, but sometimes much larger. Each body is oval or round, its size being from 1 to 2μ in diameter (fig. 4). The parasites were studied in films fixed with Schaudinn's or Flemming's fluid and stained with Heidenhain's iron-haematoxylin. In stained preparations each individual body

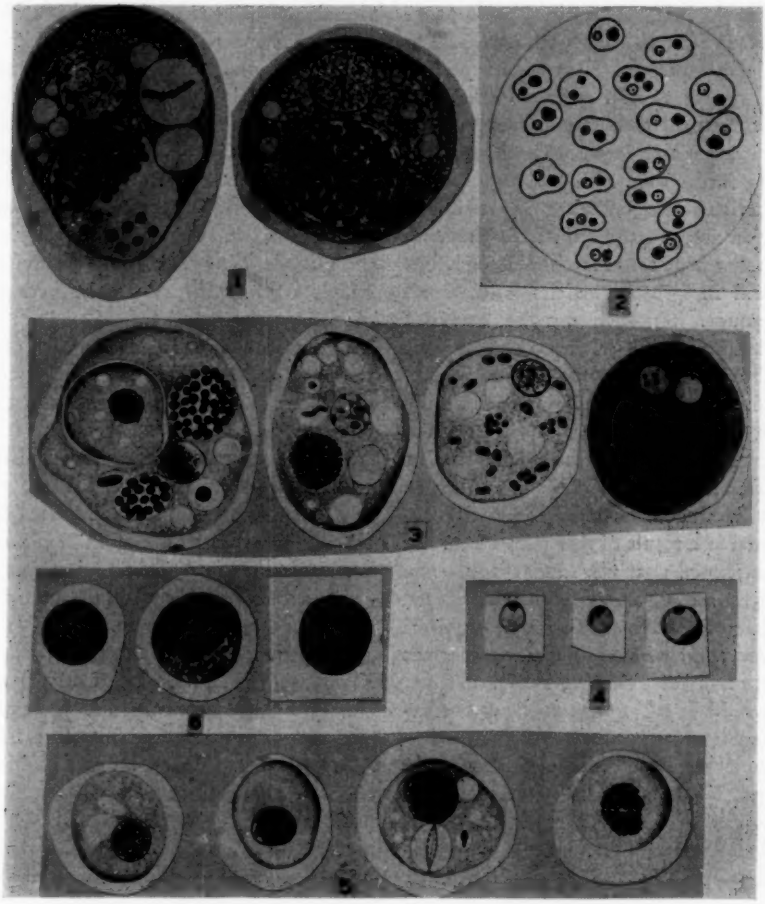


FIG. 1. CYTOPLASMIC PARASITES—SPHAERITA IN ENDAMOEBA PITHECI
FIG. 2. GROUP OF ENDAMOEBA CITELLI IN A MICROSCOPIC FIELD. CYTOPLASM OF AMOEBAE INVADED BY SPHAERITA
FIG. 3. ENDAMOEBA CITELLI WITH SPHAERITA IN ITS CYTOPLASM
FIG. 4. SEPARATE PARASITES OF SPHAERITA IN ENDAMOEBA CITELLI
FIGS. 5 AND 6. NUCLEOPHAGA IN NUCLEUS OF ENDAMOEBA CITELLI

is seen to possess a clear interior and a conspicuous membrane staining deeply with haematoxylin. Each of these bodies has on one side or on both, crescent-shaped thickenings intensely stained with iron-haematoxylin. In some parasites large vacuoles are present, situated at one end of the organism. In certain individuals one sees near the membrane a deeply staining granule which is probably the nucleus of the parasite (fig. 4).

Sometimes the parasites are arranged singly in the protoplasm of the amoeba, each being from 2 to 2.5μ in diameter, but identical in structure with those united into groups. Since the parasites occupy a considerable volume of the cytoplasm, it is probable that they impede normal metabolism in the host. Enlarging in size they at last destroy the body of the amoeba. The large numbers of these parasites present in *Endamoeba citelli* suggest the possibility that this amoeba is being gradually extermined as a result of this parasitism. It is to be noted that the same cytoplasmic parasites are of common occurrence in amoebae of the American ground-squirrel (*Citellus tridecemlineatus*) and are present in large numbers (Becker, 1926).

It would be of interest to carry out experiments on the influence of these parasites upon the development of amoebae in the intestinal canal of the host. It might be possible to use these hyperparasites of amoebae to control the pathogenic protozoa of man's intestine (Lwow, 1925).

So far as their systematic position is concerned, the question is still uncertain. Most workers believe these parasites to be Chytridia and place them in the genus *Sphaerita*. I found (Sassuchin, 1931) in the same amoeba (*E. citelli* from the suslik) parasites which attacked the protoplasm as well as the nucleus of the host (figs. 5 and 6). At the initial stages of infection one may observe at the periphery of the nucleus one or several parasites, measuring from 1 to 2 microns in diameter. In fixed and stained preparations they show very little internal structure, but in some individuals one can easily distinguish a deeply staining granule, which is probably the nucleus of the parasite. The parasites multiply within the nucleus of the amoeba and completely fill it. The nucleus undergoes hypertrophy, enlarging sometimes to twice the normal size. As a direct consequence of nuclear hypertrophy the whole protoplasm increases in quantity and the nuclear membrane becomes invisible, which is undoubtedly the last stage in the life of the amoeba.

The morphological peculiarities of the parasite, and the effect it exerts upon its host permit us to place it in the genus *Nucleophaga*.

The hyperparasites of pathogenic Mastigophora were first seen by Wenyon (1907) in *Trichomonas*. Cunha and Muniz (1923) observed the parasites also in *Trichomonas*. W. Yakimoff (1929) found hyperparasites (*Micrococcus batrachorum*) in the cytoplasm of *Trichomonas batrachorum*.

We have observed (Sassuchin, Popow, Kudrjawzew, and Bogenko, 1930) more than once parasites in the protoplasm of *Trichomonas muris* from the intestine of *Mus musculus*. In their morphological characters, structure and position in the host, they closely resemble the hyperparasites of amoebae belonging to the genus *Sphaerita* (fig. 7). In certain instances the parasites were irregularly scattered through the protoplasm of *Trichomonas*, but the dimensions, shape and structure of each parasite were similar to those described above (fig. 5). We could not definitely identify the parasites of amoebae with those of flagellates, but it seems very probable that they are closely related.

We have also observed parasites re-

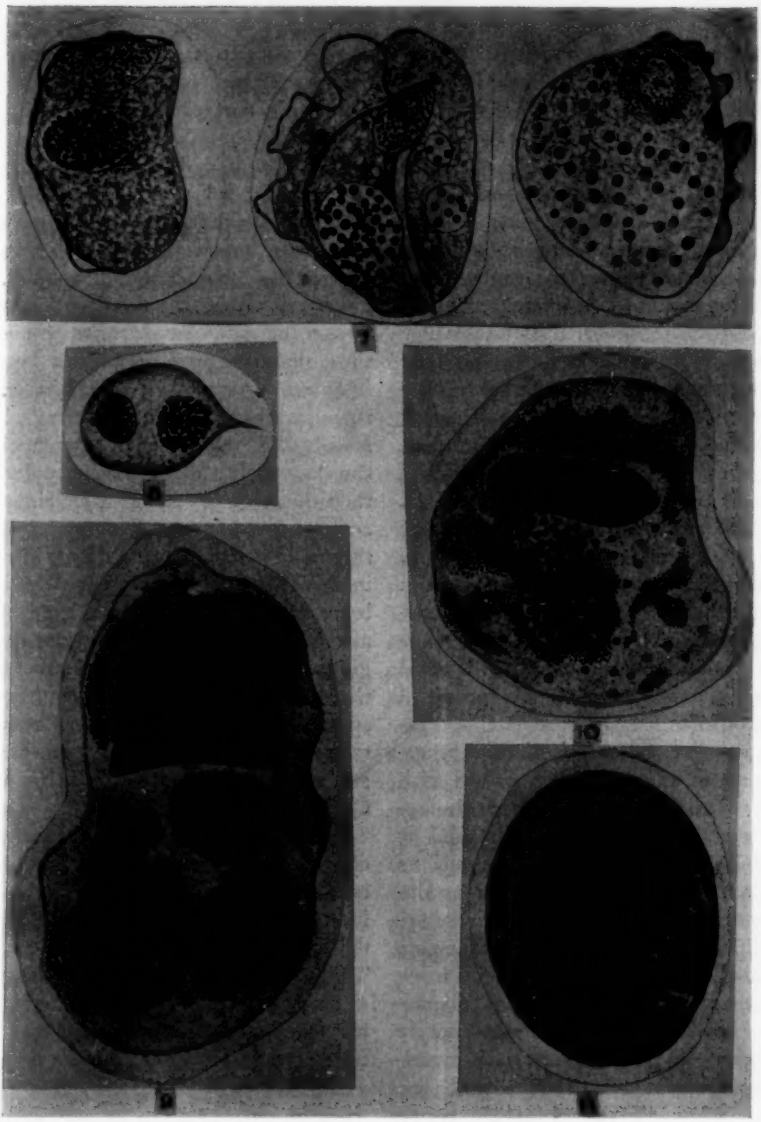


FIG. 7. CYTOPLASMIC PARASITES IN TRICHOMONAS MURIS
FIG. 8. CYTOPLASMIC PARASITES IN CHILOMASTIX MAGNA
FIGS. 9 AND 10. CYTOPLASMIC PARASITES IN NYCTOTHERUS OVALIS (SECTION)
FIG. 11. "SPORANGIUM" FROM CYTOPLASM OF NYCTOTHERUS OVALIS, DRAWN SEPARATELY

sembling those of *Trichomonas* in *Chilomastix magna* Becker, 1926. In this case, however, we have not had sufficient material to study and describe them in detail (fig. 8).

In 1925 I had an opportunity of observing two kinds of hyperparasites in the cytoplasm of a ciliate, *Nyctotherus ovalis*, from the intestine of *Periplaneta orientalis* (Sassuchin, 1928). Some were quite similar to those described above, the others were coccoid organisms. Not infrequently both kinds of parasites occurred simultaneously in the host, though sometimes they were seen separately. To the first kind belonged spherical structures, resembling sporangia, about 30 microns in diameter, surrounded by a thick membrane. These sporangia contained masses of spores (figs. 9, 10 and 11). Such sporangia occurred either singly or collected into small groups. Sometimes as many as nine were seen in the body of a ciliate. The other structures, which were found in *Nyctotherus ovalis*, were only the developmental stages of the same parasite. At the initial stages of infection one may observe separate spores of the parasite in the protoplasm of the ciliate. When stained with iron-haematoxylin or alizarin-toluidin-blue, a single spore appears, ovoidal or ellipsoidal in shape, 1.5μ broad and 2μ long, with a distinct membrane, and staining pinkish-yellow with alizarin. In properly differentiated preparations the spore membrane appears to be uniformly thick throughout, but the cytoplasm is compressed by a large vacuole and consequently the contents of the spore seem to be essentially thickened towards one end. The presence of a nucleus in these spores is still questionable. Such spores may be observed in fully formed sporangia, lying within the membrane and outside the sporangium either in the lumen of the intestine or, as was demonstrated, in the cytoplasm of the ciliate.

The subsequent stages of the parasite are represented in my preparations by sporangia in early stages of development. Such a sporangium is a cytoplasmic body containing numerous small nuclei. The size of a sporangium varies from 10 to 25 microns in diameter. It is always enclosed by a membrane, which is thicker in larger and correspondingly thinner in smaller sporangia. In form, the sporangia are usually spherical or ellipsoidal. In my preparations there are, it appears, younger stages of development, similar to those described by Chatton and Brodsky in *Sphaerita* parasitic in *Amoeba limax*. In these stages the parasite appears to be an amoeboid body with one or two nuclei of the karyosome type. Nuclear division then takes place, so that a multinucleate amoeboid sporangium is formed. While this multinucleate amoeboid body increases in size, the gradual thickening of its membrane is taking place, its maximum thickness being attained in the mature sporangium. The cytoplasm enclosed within the membrane segments into numbers of spores. A similar process has been described by Dangeard in *Sphaerita endogena*, and several authors have seen it in other Chytridia.

The size of a mature sporangium, which depends on the size of the amoeboid body, ranges from 20 to 30μ. The vast majority of individuals are spherical, more rarely ovoidal and exceptionally irregular in shape. The membrane of a fully grown sporangium attains a thickness of 1 micron. The further fate of such a sporangium may vary. In certain cases its membrane ruptures within the body of the ciliate; in others the sporangium escapes into the lumen of the intestine after the death of the ciliate. I have observed several times the emergence of spores from the sporangium within the body of the host. In preparations stained with iron-haematoxylin this stage appears as follows: by rupture of the membrane

at one end, the spores are set free in the cytoplasm, and are then dispersed by cytoplasmic streaming through the whole body of the ciliate. Some spores remain within the sporangium whose wall visibly fades away. Such a half-empty sporangium, or rather its membrane, may remain intact in the cytoplasm of the host. I have observed many of the stages described during life in a moist chamber, wherein the ciliates lived as long as 12 days in a droplet of intestinal contents diluted with physiological salt solution or with Ringer-Lock's fluid.

The harmful effect of the parasite upon the ciliate host was noticed only when, by increasing in size, it filled a large area in the ciliate. When located at the posterior end of the ciliate, the parasite may occupy one third of its body and at last causes the death of its host. First of all the sporangia exert a mechanical pressure upon the cytoplasm, and sometimes upon the macronucleus of the host. Then the invaded ciliates exhibit striking changes in their physiological processes. The contractile vacuoles pulsate sluggishly as compared with those of normal individuals. The contraction is correspondingly slower in those ciliates in which the larger amounts of cytoplasm, especially at the posterior end, are occupied by the parasites. The parasites prevent the normal circulation of food-vacuoles in the cytoplasm of the host. It is highly probable that all this taken together influences the formation of food-reserve materials by the ciliate. The change in number of glycoproteid granules is especially noticeable. These often occur in abundance dispersed through the whole cytoplasm in the form of oval granules that appear to be somewhat flattened on one side. During the growth of the parasite the number of these granules decreases gradually, until at last they disappear. At later stages changes take place in the macronucleus. The coarse round lumps disintegrate into a number of small granules. In the last moments of life these granules are in violent movement; then they become fewer and fewer, and the macronucleus finally seems to become empty. The lashing motions of the cilia become more and more sluggish, and the ciliates cease to progress. The movement of cilia gradually terminates, and at the same time the contractile vacuole ceases to pulsate. After this the cytoplasm disintegrates rapidly and the spores are set free. It is to be noted that when the sporangium ruptures within the cytoplasm of the host, the latter succumbs almost immediately.

In certain cases parasites occur in the cysts of this protozoon.

In some individuals of *Nyctotherus ovalis* taken from the same material I found in the cytoplasm many granules which I mistook at first for cytoplasmic inclusions. These are extremely small bodies, round in shape and about 0.3μ in diameter (figs. 9 and 10). They do not occur singly but are arranged in groups of different shapes and sizes. Such groups are irregularly scattered through the body of a moving ciliate, or its cyst; and may occupy the greater part of the host. When stained, the separate bodies are distinctly visible, but show very little internal structure. In living organisms the groups are fairly distinct because of their refringence. *Intra vitam*, they stain feebly with Janus green and brilliant cresyl blue, and do not stain at all with neutral red.

It is of interest to mention the arrangement of these inclusions in the cytoplasm of a ciliate in which the parasite *Sphaerita* occurs. In figure 8 one sees a sporangium whose surface is completely covered with these bodies as though surrounded by a capsule. It is to be noted that in the earliest stages of development of the parasite both the inclusions and the parasite

itself lie freely in the cytoplasm without any connection with one another. But with the growth of *Sphaerita*, when it begins to occupy a large proportion of the cytoplasm of its host, these bodies gather near the surface of the sporangium.

At the first moment of observation I was doubtful about the nature of these inclusions. To determine whether they were cytoplasmic granules of the chondriosome type, volution granules or glycoproteid bodies, specific methods of staining and several microchemical analyses were carried out. The chondriosomes in *Nyctotherus ovalis* are small, rod-shaped bodies, more or less uniformly distributed throughout the cytoplasm (Sassuchin, Ostroumow). The mentioned bodies did not show typical glycogenic staining with Best's carmine method, nor did they give a characteristic glycoproteid reaction with Fischer's safranin-tannin stain. They were insoluble in ptyalin and did not show the staining characteristic of glycogen and of glycoproteid bodies as a result of treatment with iodine solution. Mayer's method to demonstrate volutin granules (methylene blue + H_2SO_4) and the reaction with I + H_2SO_4 also did not give a characteristic staining reaction. Their resistance to fat solvents (equal portions of ether, acetic acid and 100 per cent alcohol) and a negative reaction with Sudan III after fixation with 10 per cent formalin, revealed that they were neither chondriosomes nor fat bodies.

Having observed clumps of these inclusions in living ciliates confined in the moist chamber, I noticed that they were increasing both in size and in number. This suggested the idea that a multiplicative process takes place among them. The inconstant presence of these bodies in ciliates, the absence of a food vacuole enclosing them, their increase in size, their situation in the cytoplasm, when another parasite (*Sphaerita*) occurs, as well as their presence in the encysted form, all this taken together induces me to believe that these bodies are neither food particles, nor foreign particles ingested by the ciliates. They appear to be living organisms, probably bacteria, which may multiply within their host's body. The presence of these bodies in certain individuals only affords evidence for the belief that we here see the phenomenon of parasitism rather than that of symbiosis.

PROTOZOAN PARASITES

Besides bacteria and fungi, Protozoa themselves may parasitize other Protozoa. Doflein discovered Mastigamoebae in the cytoplasm of a free-living ciliate, *Stentor*. The developmental stages of certain Suctoria (*Sphaerophrya*) take place in the cytoplasm of *Paramoecium*. These parasites are also known within parasitic ciliates. Lutz and Splendore (1908) described a microsporidian, *Nosema balantidii*, in *Balantidium* sp., parasitic in the cloaca of *Bufo marinus*.

Parasitic Microsporidia are known in gregarines. Leger and Duboscq (1909) found a microsporidian in the cytoplasm of *Frenzelina conformis*, a gregarine parasitic in the intestine of a crab, *Pachygrapsus marmoratus*. This microsporidian is found in different developmental stages of the gregarine, including its encysted forms. The crab's tissues are free from infection. The microsporidian is easily recognized in fixed and stained preparations. Under low magnification the microsporidia appear in small granules scattered throughout the cytoplasm of the gregarine. The structure of the spores is similar to that of *Nosema bombycis*, the average length being 2.8 microns.

Another microsporidian, *Perezia lankesteriae*, attacks the cytoplasm of *Lankesteria ascidiae*, a gregarine parasitic in the intestine of *Ciona intestinalis*. This microsporidian, as well as *Nosema frenzelinae*, never invades the host's tissues but occurs only in the cytoplasm of the gregarine.

A microsporidian, *Nosema marinus*, is a form of still more interest. It occurs in the cytoplasm of a myxosporidian parasitic in fish, *Coris julis* and *Coris giofredi*.

Parasites are also known in the bodies of gregarines from the intestine of Polychaetae for which Caullery and Mesnil (1919) created the separate family Metchnikovellidae. As a typical form of this family the authors have described *Metchnikovella spionis*, parasitic in a gregarine, *Polyrhabdina*, from the intestine of *Spio martinensis*.

The systematic position of these parasites of gregarines is uncertain. Some observers consider them to be allied to the Microsporidia; others believe them to be closely related to the Ascomycetes (Caullery and Mesnil) or to the Haplosporidia (Averintzev).

A METAZOAN PARASITE

Lastly, of particular interest is in my opinion the finding in a protozoan host of a metazoan parasite. Schubotz has found a nematode in the cytoplasm of a ciliate, *Pycnothrix monocystoides*, from the intestine of *Hyrax capensis*.

CONCLUSION

In studying the life-cycle and cytology of Protozoa, we should not forget that parasites may be present. They often confuse the laboratory worker, and are sometimes a cause of grave mistakes. It is sufficient to recall that Walker mistook parasites of *Nyctotherus ovalis* (described above) for one of the developmental stages of this ciliate; while Goldschmidt interpreted the cytoplasmic parasites of *Mastigina* as extranuclear chromatin.

Parasites are enemies of mankind, but the parasites of parasites are our friends. It is probable that in certain cases they help the infected host to conquer his infection. We should, therefore, not neglect these hyperparasites but study them more thoroughly, since they deserve careful investigation.

LIST OF LITERATURE

(1) Bütschli, O. 1882–1889. Protozoa. Bronn's Kl. u. Ordn. d. Thier—Reichs. *Leipzig.*

(2) Chatton, E., and Brodsky, A. 1909. Le parasitisme d'une chitridinée du genre *Sphaerita* Dangeard chez *Amoeba limax* Dujard. Étude comparative. *Arch. Protist.*, XVII, i.

(3) Cragg, F. 1919. A contribution to our knowledge of *Entamoeba coli*. *Ind. J. Med. Res.*, V, 301.

(4) Cunha, A. da, and Munitz, J. 1923. Parasitismo de *Trichomonas* por chytridacae do genero *Sphaerita* Dangeard. *Brazil—Medico*, XXXVII, 15.

(5) Dobell, C. 1919. The Amoebae Living in Man. *London.*

(6) Entz, G. 1913. Über Organisationsverhältnisse von *Nyctotherus piscicola* (Daday), *Arch. Protist.*, XXIX, 364.

(7) Epstein, H. 1922. Über parasitische Infection bei Darmprotozoen. *Arch. Russes de Protistolog.*, I.

(8) Kudo, R. 1924. A biologic and taxonomic study of the microsporidia. *Illinois Biolog. Monogr.*, IX, 2–3.

(9) Lwoff, A. 1925. Chitridinées parasites des amibes de l'homme. Possibilité de leur utilisation comme moyen biologique de lutte contre la dysenterie amibienne. *Bull. Soc. Path. Exot.*, XVIII, 18.

(10) Nöller, W. 1922. Die wichtigsten parasitischen Protozoen des Menschen und der Tiere. *Berlin.*

(11) Sassuchin, D. 1925. Zur Kenntniss der Plasmazinschlüsse bei den Opalinen. *Arch. Russes de Protistolog.*, III.

(12) Sassuchin, D. 1928. Zur Frage über die Parasiten der Protozoen. I. Parasiten von *Nyctotherus ovalis* Leidy. Arch. f. Protist., 64, 1/2.

(13) ———. 1928. Zur Frage über die ecto-und entoparasitischen Protozoen der Froschkaul quappen. Arch. Protist., 64, 1/2.

(14) ———. 1931. Zum Studium der Darmprotozoen fauna der Nager im Süd—osten KSFSR. I. Darmprotozoen des *Citellus pygmaeus* Pall. *Arch. Protist.*, 74, 3.

(15) Sassuchin, D., Popoff, P., Kudrjwzew, W., und Bogenko, W. 1930. Über parasitische Infektion bei Darmprotozoen. *Arch. Protist.*, 71, 2.

(16) Walker, E. 1909. Sporulation in the parasitic Ciliata. *Arch. Protist.*, 17, 297.

(17) Wenyon, C. 1926. Protozoology. *London.*

(18) Yakimoff, W. 1931. Bolesni domaschnick schiwotnich wisiwaemie prosteischimi (Protozoa) (in Russian).

NEW BIOLOGICAL BOOKS

The aim of this department is to give the reader brief indications of the character, the content, and the value of new books in the various fields of biology. In addition there will frequently appear one longer critical review of a book of special significance. Authors and publishers of biological books should bear in mind that THE QUARTERLY REVIEW OF BIOLOGY *can notice in this department only such books as come to the office of the editor. The absence of a book, therefore, from the following and subsequent lists only means that we have not received it. All material for notice in this department should be addressed to Dr. Raymond Pearl, Editor of* THE QUARTERLY REVIEW OF BIOLOGY, *1901 East Madison Street, Baltimore, Maryland, U. S. A.*

BRIEF NOTICES

EVOLUTION

FUNCTIONAL AFFINITIES OF MAN, MONKEYS, AND APES. *A Study of the Bearings of Physiology and Behaviour on the Taxonomy and Phylogeny of Lemurs, Monkeys, Apes, and Man.*

By S. Zuckerman. Harcourt, Brace and Co., New York. $3.00. 8½ x 5½; xviii + 203; 1933.

This book is an appropriate sequel to the author's recent *The Social Life of Monkeys and Apes* in which are continued his studies of the broader aspects of the interrelationships of the primates. A not unsuccessful attempt is made to allocate the phylogenetic position of the primates on the basis of such functional and physiological characteristics as the mechanisms of reproduction, blood reactions, receptor organs, behavior patterns, diseases and parasites, hybridization, and cortical physiology. On the whole the phylogenetic implications of this original method of classification are in agreement with the more orthodox taxonomy based upon morphology. The book is well written, contains an extensive and very valuable bibliography, and an index.

FOSSIL FLORAS OF YELLOWSTONE NATIONAL PARK AND SOUTHEASTERN OREGON. *Contributions to Palaeontology. Carnegie Institution of Washington Publication No. 416.* Containing following monographs: *Fossil Floras of Yellowstone National Park. Part I. Coniferous Woods of Lamar River Flora*, by Charles B. Read; *The Trout Creek Flora of Southeastern Oregon*, by Harry D. MacGinitie.

Carnegie Institution of Washington, D. C. $1.50 (paper); $2.50 (cloth). 10 x 6¾; 68 + 16 plates; 1933.

There are two monographs in this volume, one on fossil trees and the second on fossils of the small flora. The last adequate account of the plant fossils from the Yellowstone area, by Knowlton, was published in 1899, so that it seems to be time to bring matters up to date. There are six plates of microscopic sections from the fossil trees and 16 plates of seeds and leaf prints, all extremely good.

Dr. Read concludes that the genus *Pinus* was established by Upper Eocene or Lower Oligocene times. Dr. MacGinitie emphasizes the resemblance between the Miocene forest of the Trout Creek region of Oregon and the living floral association of northeastern Asia (Japan and Manchuria).

THE EVOLUTION OF MORALITY.

By George Whitehead. John Bale, Sons and Danielsson, London. 10s. 6d. net. 8⅜ x 5⅝; iii + 340; 1933.

The thesis of this book is that morality has never rested on religious sanctions and that it has its roots in animal behavior. Unfortunately, Mr. Whitehead has just two means of studying animal

behavior: one to imagine what animals would do if only they were Englishmen crawling on all fours, the other to pile up quotations from books written by other bookish men. Neither of these methods seems to have led him to any new conclusions. He rises to heights of eloquence only when he denounces women, war, and religion. At other times he is pretty tiresome.

THE GENERAL THEORY OF EVOLUTION.
By Malcolm MacTaggart. W. Heffer and Sons, Cambridge. 1s. 6d. net. 7¼ x 5; vi + 50; 1933 (paper).

Starting with little and figuratively adding nothing the author amuses himself in a metaphysical manner throughout some fifty pages by toying abstractly with profundity and foolishness, by laughing once at the absurdity of pretentious moral suasion, and concluding by asking a few questions which he regards as unanswerable. The subtle art of engaging a reader's interest or imagination finds no place in the rattle of words in which the evolutionary events as given by modern science are held to follow the preconceived logical system of Hegel. *Trust* as opposed to *belief* is given as the ideal that will enable human evolution to proceed beyond its present state.

MAN AND THE VERTEBRATES.
By Alfred S. Romer. University of Chicago Press, Chicago. $3.00. 9 x 6; vii + 427; 1933.

A brief, comprehensive survey of vertebrates and human evolution written for biological students at the University of Chicago under the new plan of college work. The text serves as outside reading for those students attending the author's lectures on the vertebrates and on the human body. The volume is extensively illustrated. Many of the views of fossil remains and reconstructed groups in museums have not hitherto appeared in text books. The volume contains no bibliography but is indexed.

AN INTRODUCTION TO THE STUDY OF FOSSILS (*Plants and Animals*). *Revised Edition.*
By Hervey W. Shimer. The Macmillan Co., New York. $4.00. 7¾ x 5¼; xviii + 496; 1933.

This is the second edition of a textbook intended for college students who begin the study of paleontology without previous work in biology. Accordingly, the description and discussion of living plants and animals goes side by side with the treatment of fossil forms of the same phyla. It is well illustrated and has an excellent index.

GENETICS

NATURE AND NURTURE.
By Lancelot Hogben. W. W. Norton and Co., New York. $2.75. 8½ x 5⅜; 144; 1933.

This book, originally delivered as a series of William Withering Memorial Lectures at the University of Birmingham, covers somewhat the same ground as the author's *Genetic Principles in Medicine and Social Science*, which was noticed in Volume VII, page 477, of this REVIEW. However, it lays more emphasis on statistical methods appropriate to the study of human genetics and less on dubious generalities than did the latter book. The use in genetic analysis of the Principle of Random Mating and of the study of consanguineous parentage and familial diseases is illustrated. The author emphasizes the interdependence of nature and nurture, and concludes that while the correlation technique may show the existence of gene differences whose manifest effect is not affected by differences of environment to which different members of a population are exposed

The belief that a comparison between observed correlation of relatives and correlations based upon purely genetical assumptions provides us with a measure of the influence of nurture is not justified, because of the close relationship between the distribution of gene differences and differences due to environment in populations of viviparous animals which live in families, especially when, as with human populations, the environment of different families may differ greatly.

In so far as a balance sheet of nature and nurture has any intelligible significance, it does not entitle us to set limits to changes which might be brought about by regulating the environment.

VERERBUNGSLEHRE. *Mit besonderer Berücksichtigung der Abstammungslehre und des Menschen. Zweite Auflage. Band II: Sexualität und allgemeine Probleme.*

By Ludwig Plate. Gustav Fischer, Jena. 30 marks (paper); 32 marks (cloth). 9⅝ x 6½; xiv + 678; 1933.

This is the second volume of a series of three of the second and expanded edition of the author's masterly *Vererbungslehre*. Sexuality and problems relating to it are discussed in this volume, 361 pages being devoted to special discussions and 263 to theoretical problems. The author develops the material in the same thorough manner which characterized the first volume noticed previously in these columns (Vol. VIII, p. 103). A bibliography of 28 pages is appended.

GENERAL BIOLOGY

CHARLES DARWIN'S DIARY OF THE VOYAGE OF H.M.S. "BEAGLE."

Edited from the MS by Nora Barlow. The Macmillan Co., New York. $6.50. 9⅛ x 6⅛; xxx + 451; 1933.

This volume is a documentary contribution of first class importance to the history of biology. Since its first appearance in 1839 Darwin's *Voyage of the Beagle* has been one of the most widely read books on natural history ever published. It is now justly regarded as one of the world's great classics. But hitherto all that we have had is the finished work, as Darwin gave it to the world.

The volume now before us, edited with the most painstaking care and accuracy and a fine sense of the highest type of bibliographic scholarship by one of Darwin's granddaughters, gives the complete text of the original diaries—"eighteen little pocket-books"—in which Darwin made his daily notes and from which he composed the *Journal of . . . . the Voyage . . . .* for publication. It is a superb production, from every point of view. It contains such homely details as that at the next opportunity there are to be purchased "night-caps," "2 lbs. common soap," etc. It shows how Darwin's ideas changed about evolutionary problems. It shows how bad a speller a very great man may be. Altogether it is a great book, which no biological library, public or private, can be without.

DYSHARMONIES ET DISCONTINUITÉS DANS LA CROISSANCE. *Actualités Scientifiques et Industrielles 95. Exposés de Biométrie et de Statistique Biologique I.*

By Georges Teissier. Hermann et Cie, Paris. 10 francs. 9¼ x 6⅛; 39; 1934 (paper).

In the first of a series of monographs on mathematical biology Teissier describes the researches on the relative growth of the different parts of an organism which have been made by various workers, notably by Huxley and by Teissier himself. The rate of growth of one organ in a wide variety of forms is found to be either equal or proportional to that of other organs. This law of growth may be derived from the assumption, for which there is experimental evidence, that the rate of growth of an organ is proportional to the mass of the organ and to the amount of food available. In some cases the rate of relative growth changes abruptly at some stage in the development of the organism. This change may perhaps be the result of the coming into action of new hormones, although this hypothesis is not yet definitely confirmed by experimental evidence. Altogether this is an interesting account of a line of work which may shed new light on the complex problem of growth. There is a bibliography of one page.

THE LIVING WORLD. *An Elementary Biology.*

By Helen G. Mank. Benj. H. Sanborn and Co., Boston. $1.68. 7½ x 5⅜; xxiv + 673; 1933.

A book is here offered for high school pupils which aims to teach them to ob-

serve accurately. To this end, the text itself does not give the information to answer all the questions but it must be supplemented by observation, other books, and the teacher. Purposely, much more material is given than can be used in a single course; part of this is arranged as additional work for quick pupils. Many useful and interesting teaching devices are included. We would personally take exception to some of the statements made, such as part of the section on alcohol. Throughout the book there is considerable emphasis and space devoted to the public health aspect of biology which is surely laudable. As a whole the book seems somewhat uneven—some parts are very simple and some too advanced for most high school pupils. Although the author states that the book has grown out of an actual course, it seems rather too ambitious in scope and material required for many schools.

THE SCIENCE OF RADIOLOGY.

Edited by Otto Glasser. Charles C. Thomas, Springfield, Ill. $4.50. 9½ x 6¼; xiii + 450; 1933.

Twenty-eight American scientists have contributed to this extremely fine book on radiology. It is part of the program of the radiologists developed in connection with the Century of Progress Exposition and the first International Congress of Radiologists. It is edited by and the first two chapters are written by Otto Glasser. Apparently everything is here —history, physics, apparatus, use. Some of the chapters are highly technical, but they contain just the sort of information one wants. Muller has an excellent chapter reviewing his x-ray induced mutations and Packard has summarized his work on the biologic effects of x-rays. The bibliographies are an especially valuable feature. There are both name and subject indices.

CAVERNS OF VIRGINIA. *Commonwealth of Virginia State Commission on Conservation and Development, Virginia Geological Survey, Bulletin 35, Educational Series No. 1.*

By William M. McGill. Virginia Geological Survey, Box 1428, University, Va. $1.00 plus postage. 10⅝ x 7¼; xvi + 187; 1933.

The western portion of Virginia is honeycombed with caverns of an unusual and striking character which attract a large number of visitors throughout the year. This book has been prepared by the Virginia Geological Survey to give to the interested individual a general knowledge of the geological history and physiography of the Appalachian Valley, of methods of cave formation, and of their characteristics. All of the important developed caverns are described in detail. The volume is excellently illustrated with photographs and maps and contains a glossary, a literature list and an index.

SYMBIOSE, PARASITISME ET ÉVOLUTION (*Étude Mathématique*). *Actualités Scientifiques et Industrielles 96. Exposés de Biométrie et de Statistique Biologique. II.*

By V. A. Kostitzin. Hermann et Cie, Paris. 15 francs. 9¾ x 6⅞; 46; 1934 (paper).

In this interesting study the author develops for the special cases of symbiosis and parasitism various modifications of Lotka's and Volterra's equations for the evolution of a system of species. Applying his equations to Pérez's distribution of number of visceral sacs of *Chlorogaster* in parasitized *Pagurus* he concludes that this is not a case of multiple parasitism but of the budding of a single parasite. There is a bibliography of 17 titles.

MÉTHODES PHYSIQUES EN BIOLOGIE ET EN MÉDECINE.

By P. Lecomte du Noüy. J.-B. Baillière et Fils, Paris. 22 francs. 8¼ x 5⅛; 194; 1933 (paper).

A simple exposition of the physical methods, instruments and measurements more commonly used by the student of biology or medicine. In very brief form

the author treats of thermostats, density, cryoscopy, surface tension, viscosity, hydrogen ion concentration, electrical conductivity, optical methods, and spectrophotometry. A useful laboratory reference work.

PRÉCIS DE MICROSCOPIE. *Technique. Expérimentation. Diagnostic. Cinquième Édition Entièrement Refondue.*

By M. Langeron. Masson et Cie, Paris. 100 francs. 7½ x 5; xx + 1205; 1934.

This is the fifth edition of an introduction to the use of the microscope in the study of parasitology with the emphasis laid on microscopy as an aid to diagnosis. Methods for the study of most of the phyla of the animal kingdom are given and there are also sections devoted to bacteriology and to plant histology. It is illustrated and has an index.

NACHWEIS DER BIOLOGISCH WICHTIGEN KÖRPER DURCH FLUORESZENZ UND FLUORESZENZSPECKTREN. *Handbuch der biologischen Arbeitsmethoden. Lieferung 420.*

By Charles Dhéré. Urban und Schwarzenberg, Berlin. 11.50 marks. 10 x 7; 210; 1933 (paper).

Since *Lieferung* 40 dealt in some detail with the physical equipment used in studies on fluorescence this number is for the most part limited to the applications of this branch of spectroscopy to the study of relatively pure solutions of biochemically important substances. Methods for the investigation of tissues and body fluids are not given.

THE ORIGIN OF LIVING MATTER.

By H. A. Gray and N. M. Bligh. W. Heffer and Son, Cambridge. 1s. 6d. net. 7¼ x 4⅞; iii + 27; 1933 (paper).

According to the authors the energy of momentum resulting from the detachment of the moon from the earth led to the formation of bi-nuclear or "Vital" atoms. This theory, they state, "will explain and account for all and every phenomenon of vitalism;" just how is not entirely clear to us.

HUMAN BIOLOGY

LA COSTITUZIONE INDIVIDUALE. *Dottrina. Metodo. Tipi Morfologici. Volumes I and II.*

By G. Viola. Licinio Cappelli, Bologna. L. 100. 10 x 6¾; Vol. I, xx + 455; Vol. II, v + 397; 1933 (paper).

The concept that the somatic structure of the individual is related to the organic structure and so indicates the predisposition of the individual to disease was revived by Benecke and De Giovanni about 50 years ago. This, the soundest interpretation of medical constitution, is now maintained in Europe only by Viola and his students.

In these volumes are collected the majority of his writings since 1902, in which he has developed this concept especially with regard to the anthropometric method of determining the morphologic types. The work consists of three parts. The first deals with the history and theories of constitution, which the author defines as "the science of the correlated anatomical and functional, physical and psychic characters of the individual."

The second part is very important for its discussion of the difference between constitutional type and anomaly and disease. Here is an excellent criticism of the weakness inherent in the genetic concept of J. Bauer and others.

In the third part are collected his articles on anthropometric measurements. He has devised a special apparatus to be used instead of the anthropometer and apparently more satisfactory for laboratory purposes. The measurements taken that he considers have an anatomical and physiological significance are only nine for the trunk and two for the limbs. From the constants calculated on 350 Venetian male adults he has derived a system of gradation that permits a comparable classification of all individuals.

In this schematic review, justice cannot be done to other important articles which contain the results of investigation on

disease associated with bodily types, the correlation of external measurements with roentgenograms of different organs, etc. There is also an excellent review of the writings on the evolutionary significance of bodily habitus.

No student of human constitution can do without consulting this work which illustrates the basic scientific method necessary for future research.

THE SOCIAL COST OF INDUSTRIAL INSURANCE. *By Maurice Taylor. Alfred A. Knopf, New York.* $3.25. 8 x 5⅝; xxxviii + 421; 1933.

This investigation deals with a social problem of importance which has never been sufficiently considered. The so-called industrial insurance is a special form for people with small incomes, which does not require medical examination and is sold at small weekly premiums. These are collected by the agents, whose salesmanship is of the high pressure variety. It becomes thus relatively expensive for both companies and the policyholders. The result, as even a casual observer will have noted, is that after a period the varying economic state of the insured may force him to ask for cash value or to lapse. In either case he has lost by the transaction. The purpose of this study is to measure this loss, which for the period 1928–1932 the author estimates (for lapsed insurance alone) at almost 200 million dollars. The material is derived almost wholly from the records of three large insurance companies, which may explain why on page 153 the chapter heading ends with an interrogation point: "Do the companies gain from lapses?"

The subject matter includes a brief historical note on the origin of this form of insurance policy, followed by a very clear outline of the difference between it and the ordinary policy. The author proceeds to give the extent of its development in this country and geographical distribution of the insured. Especially well done are the chapters on the analysis of the cost, which is compared with that of the ordinary form, and his proposals in regard to families dependent on public welfare. His general recommendations include a lowering of the cost with greater consequent benefits to the policy holders, the limitation of sales in ratio to the income, etc. Some of these recommendations are useless, we feel, because unless paternalism increases, a change of method will depend wholly on the attitude of the insurance companies and their estimate of possible profit.

IN THE WAKE OF "THE BOUNTY." *To Tahiti and Pitcairn Island.*

By Charles Chauvel. Endeavour Press, Sydney. 6 shillings. 8⅜ x 5⅜; 157; 1933.

This book, a by-product of the author's film of the same name, contains a brief narrative of the mutiny of the *Bounty* and the subsequent history of the mutineers and an account of Mr. Chauvel's own experience in making the film. The most interesting part of the book is the description of the Pitcairn Islanders of today, the descendants of the mutineers. About thirty years ago the island was converted to Seventh Day Adventism, with deplorable effects.

> Their new religion has brought to them a mass of modern "taboos" as fantastic as any of the tribal inhibitions of the Polynesian savages of yore. Tea is a drug and disallowed in the homes, while to smoke publicly on the island would be an offence. Baking-soda has been condemned, and the missionaries have even tried to prevent the eating of all meat. The pig, which in the past was so prized on Pitcairn, is to-day an unclean animal, and no one is allowed to own one. All literature except religious books and tracts and a panic-stricken sheet called "The Signs of the Times" are censored from the island. Dancing is not allowed, and only religious records and nursery rhymes are encouraged on the gramophone. They have been taught to believe that the end of the world is very near at hand, and in this the Book of Revelations is followed most literally—each fresh earthquake or pestilence experienced in some part of the world being regarded as a new and definite portent that the end is in sight.
>
> The people are now so definitely rooted in this belief that no provision is made for their future; no young coconuts or breadfruit-trees have been planted, and the same applies to the timber of the island, which has been continually felled for the building of their homes and boats without thought of replanting for future needs.

THE EFFECT OF TROPICAL SUNLIGHT ON THE DEVELOPMENT OF BONES OF CHILDREN IN PUERTO RICO. *A Roentgenographic and Clinical Study of Infants and Young Children with Special Reference to Rickets and Related Factors. U. S. Department of Labor, Children's Bureau Publication No. 217.*

By Martha M. Eliot. U. S. Government Printing Office, Washington. 10 cents. 9⅛ x 5⅝; v + 122; 1933 (paper).

In a previous investigation, undertaken jointly by the Children's Bureau and the Department of Pediatrics of Yale University, it was found that in a large proportion of cases the bones of infants living in a temperate climate (New Haven, Conn.) showed sooner or later certain minor changes which were interpreted as evidence of slight rickets regardless of the fact that the infants observed had been given what was thought to be an amount of cod-liver oil sufficient to prevent rickets. The present study, of 584 infants living in a tropical country exposed the year round to intense sunlight, was made by the same investigators to determine whether or not the roentgenographic changes usually interpreted as signs of slight rickets should not be regarded as physiological variations of normally growing bone. After working over the clinical and x-ray records of both the New Haven and Puerto Rico studies, Dr. Eliot and her co-workers were able to conclude that rickets is practically absent in the tropical country, and that the bone changes previously believed to be signs of early or mild rickets are probably correct. From a scientific viewpoint it is difficult to overestimate the value of work of this character. The dividing line between the limits of physiological normality and early pathology is so nebulous and knowledge concerning it is of such importance in almost every field of medical practice that every contribution is of the greatest moment. A short summary report of the paper under review will be found in the *American Journal of Diseases of Children*, Vol. 46, p. 1237.

THE MIND OF CHINA.

By Edwin D. Harvey. Yale University Press, New Haven. $3.50. 9¼ x 6⅛; xi + 321; 1933.

This is a fundamental contribution to studies on the Chinese. The author, long a resident of China as Professor of Sociology at the College of Yale-in-China, at Changsha (Hunan Province) has had unusual opportunities to observe and study the social system of the Chinese, the influence which their profound faith in ancestor worship has upon their daily lives and customs, their extraordinary dependence on every sort of magic and their belief in the "existence of another world of spirits, a shadowy but real counterpart of life here on earth." Underdevelopment of the industrial and economic arts and overgrowth in population are two of China's most serious problems. Both of these are deeply conditioned by an inveterate animism. Renunciation of the philosophy of animism and the acceptance of the obviously effective materialism and industrialism of the West is the essence of the temper of Young China today. The masses (nearly one quarter of the world population) have merely turned the new expressions into the old animistic molds. However, a collapse of the old way of thinking and living is bound to come with the new education, the growth of railroads and industry; and because of this China will be faced with a problem of immense complexity. A new philosophy of living must be evolved. The volume is copiously documented and is indexed.

THE LIFE OF A FOSSIL HUNTER.

By Charles H. Sternberg. Charles H. Sternberg, 4046 Arizona St., San Diego, Calif. $1.75. 7⅝ x 5⅛; xiii + 286; 1931.

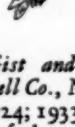
HUNTING DINOSAURS *in the Bad Lands of the Red Deer River, Alberta, Canada. A Sequel to The Life of a Fossil Hunter.*

By Charles H. Sternberg. Charles H. Sternberg, 4046 Arizona St., San Diego, California. $1.75 [Both books for $3.00]. 7⅝ x 5⅛; xv + 254; 1932.

Both of these books are reprints. *The Life of a Fossil Hunter* (first printing 1909) deals with the author's wide experience in collecting in the western part of the United States. Hunting for fossils in the seventies and eighties involved far more

than patiently searching for fruitful places to excavate. It meant danger from hostile Indians, days with little or no food, narrow escapes from drowning, etc. For eight seasons Sternberg worked with Cope in the field. This part of the book will perhaps be of the greatest interest to biologists as he writes most entertainingly of Cope and their joint experiences which were often of a thrilling character. *Hunting Dinosaurs* (first printing 1917) is a sequel to *The Life of a Fossil Hunter*. After 1912 the author and his three sons spent much time in the Red Deer region in Alberta where are to be found the richest Cretaceous fossil fields in the world.

Neither of these books is devoted merely to the author's experiences in hunting fossils. They contain much information concerning fossil beds and their contents, the manner of collecting, description and illustration of findings and methods of preparing specimens for exhibitions. Many of the finest specimens of extinct mammals in the American Museum of Natural History, in the Victoria Memorial Museum at Ottawa, as well as in various European museums are due to the enthusiastic labors of Sternberg and his assistants. The books can be recommended for general libraries, particularly high school libraries. They open up a fascinating field for embryonic naturalists. Both volumes are abundantly illustrated and indexed.



URBAN SOCIETY.

By Noel P. Gist and L. A. Halbert. Thomas Y. Crowell Co., New York. $3.50. 7⅞ x 5½; xv + 724; 1933.

This is a study of the growth and characteristics of American cities and their populations. It is less concerned with the possibilities for uplift than it is with the detailed description and interpretation of these curious animal aggregations. It is, quite literally, a study in human ecology and its plan and method are based to a large extent on ecological concepts. The study is carried out with thoroughness and considerable literary skill. The kind of information conveyed by case histories and crime statistics is not represented here; the emphasis is on the social and economic factors that influence the founding and growth of cities, on migrations to, from, and within cities, and on the effects the peculiar conditions of city life have had on human behavior. The authors have made frequent and effective use of long quotations from sociological studies of particular cities, and their data, on which charts and tables are based, are recent enough to show some of the trends of cities during the depression. It will make a good college textbook but it deserves a wider sale than that. There are a considerable number of thoughtful people whose contacts with city life have been neither close enough nor of long enough duration to give them a basis for understanding the system of coöperative competition that underlies urban life, and they should find this book useful in this respect. There are annotated bibliographies at the end of each chapter and good indexes, one for subjects and one for names of cities.

THE EMPTY QUARTER, *being a Description of the Great South Desert of Arabia Known as Rub 'al Khali.*

By H. St. J. B. Philby. Henry Holt and Co., New York. $4.00. 8½ x 5½; xxiv + 432 + 3 folding maps; 1933.

The journey of which this book is a narrative was not Mr. Philby's first exploration of the interior of Arabia. In 1917 he had crossed the peninsula from the Persian Gulf to the Red Sea—the first European since Sadlier, a century before, to make the journey—and in 1918 he had explored the Jabal Tuwaiq as far as the Wadi Dawasir but had been forced to turn back regretfully without penetrating the Rub'al Khali or Empty Quarter, the great southern desert of Arabia, "perhaps the largest blank on the map outside the Polar regions." Early in 1932 Ibn Sa'ud made him leader of an expedition which crossed the desert from the Persian Gulf to its southern border and thence westward through its most desolate portion to Wadi Dawasir. On the first part of the journey there were occasional wells, covered to protect them from the shifting sands,

but for the last 375 miles the party had to depend entirely on the water that they carried with them. The supposed ruins of the legendary city of Wabar which they visited turned out to be a meteorite crater. Appendices give reports on the meteorites and silica glass found there as well as on other geological, zoölogical and botanical specimens collected by Mr. Philby. The book also contains an index and excellent maps of the route of the expedition. This is an exciting book of adventure as well as a first rate narrative of an important scientific exploration.

ANCIENT AZTALAN. *Bulletin of the Public Museum of the City of Milwaukee Vol. XIII. By S. A. Barrett. Milwaukee Public Museum, Milwaukee.* $7.00. 10⅝ x 7; 602; 1933 (paper).

The ancient earth-works at Aztalan, situated in south-eastern Wisconsin, are among the more important archaeological sites in the United States. Although definite knowledge of their existence dates from the Black Hawk War in 1832, little actual, organized exploration and excavation has been done, with the exception of the survey made in 1850 by Dr. O. A. Lapham, until 1919 when the author of this book began his investigations.

The principal features of the site are the ridge surrounding it, the remains of a stockade, and numerous pits and mounds, only one of which yielded a burial that could be considered authentic. It had long been held that this was a ceremonial spot, but the author abandons this theory on the evidence he has collected and holds the view that it served the more prosaic purposes of defense and utilitarian service. He likewise discards the belief that the ancient inhabitants of Aztalan knew the art of making brick. His assumption is that native clay, mixed with grasses, was used to line the stockade to make it stronger as a defense, and that when it was burned, presumably by enemies, the clay baked and broke off in "bricks"—lumps irregular in form.

This publication is well illustrated with maps showing the present topography of the site, as well as those made by Dr. Lapham, and many excellent photographs of the earth-works and their contents. The author has also provided a bibliography of seven pages and an index.

HEREDITY AND ENVIRONMENT. *Studies in the Genesis of Psychological Characteristics. By Gladys C. Schwesinger. Edited by Frederick Osborn. The Macmillan Co., New York.* $4.00. 9¼ x 6¼; ix + 484; 1933.

This is a critical compendium of the studies made to determine the relative influence of heredity and environment on the development of personality and intelligence. Its value lies in the clarity of the author's views and her ability to take full cognizance of all the more important investigations.

Splitting the psychological characteristics into intelligence and personality is, as the author admits, arbitrary and evidently done only for the purpose of considering the so-called intelligence tests separately from general psychological theories. With regard to the intelligence tests, the author is rather diffuse but complete in the examination of all the literature. Her conclusion is that they are "valid and reliable," but she immediately adds: "Since many extravagant and even bizarre claims have at times been made on such topics as group differences in intelligence . . . . it is essential in interpreting such data that a proper perspective be kept." This sober outlook is characteristic of the objectivity of the book.

The part that treats of personality is, compared to the other, very schematic though in no way incomplete. We do not find here the same thorough analysis as for the intelligence tests.

Finally, the author arrives at the only conclusion possible, that is, that the investigations so far conducted cannot be said to have found an answer to the question.

This volume makes an excellent textbook and will be useful for all students of the subject.

THE AMERICAN ABORIGINES. *Their Origin and Antiquity.*

A Collection of Papers by Ten Authors, Assembled and Edited by Diamond Jenness. University of Toronto Press, Toronto. $2.50. 9¼ x 6¼; 396; 1933.

The ten papers in this volume, all by recognized experts in their respective fields, make an extremely valuable symposium on the present status of knowledge about the American Indian. While it is impossible here to review the book in detail some of the outstanding conclusions may be mentioned. W. A. Johnston is of the opinion that western migration routes to North America have been open for 25,000 to 30,000 years, much longer than any possible route in the north-east. Alfred S. Romer holds that there is no paleontological evidence suggesting the presence of man in North America earlier than the withdrawal of the last Pleistocene ice sheet. On archeological grounds N. C. Nelson reaches the same conclusion. E. A. Hooton concludes a brilliant essay on the thought that the American race is a composite race "composed of heterogeneous strains welded together by mixture," Clark Wissler is of opinion that the great variety of cultures and of traits in the New World has obscured whatever may have been transferred directly from the Old World. Roland B. Dixon refuses to allow any of the claims made for diffusion of cultures across the southern Pacific to South America.

The value of the book is seriously impaired by the absence of an index.

660 RUNAWAY BOYS. *Why Boys Desert Their Homes.*

By Clairette P. Armstrong. Richard G. Badger, Boston. $3.00. 8 x 5½; 208; 1933.

This book consists essentially of a statistical analysis of case histories, from the Children's Court of New York City, of 660 boys charged with deserting their homes. The various factors reviewed include, among others, age, intellectual ability, physical defects, nationality, education, economic status, and home conditions. Thus it was found that runaway boys have an average age of approximately 13 years and an average I. Q. of 77.7; that fifty per cent of them have nervous habits such as enuresis, masturbation, temper-tantrums, and so on; that seventy-five per cent are of foreign or mixed parentage; that fifty per cent are graded above their inherent capacities in school; that twenty per cent have both parents employed; that only forty-five per cent have both parents living and living together; that thirty per cent have either a step-mother or step-father. An interesting chapter is devoted to the boys' reasons for leaving home. Of these, excessive beatings, fear of beating and punishment, and a hatred of school or school teacher are given in over fifty per cent of the cases. It is questionable whether the subtitle of the book has been appropriately chosen.

AN ASTRONOMER'S LIFE.

By Edwin B. Frost. Houghton Mifflin Co., Boston. $3.50. 8 x 5½; xi + 300; 1933.

This is an interesting and stimulating autobiography of a distinguished astronomer, who had the devastating misfortune to go blind at the zenith of his professional career. The simple yet lofty courage with which Professor Frost met this calamity has been an inspiration to his colleagues and friends. His whole life exemplifies and illustrates the traditional virtues and abilities of the New England stock from which he stems. The Frost family, with its record of achievement in scholarly pursuits, is a perfect paradigm for the eugenist.

Professor Frost writes with clarity and charm, and his life has been an interesting one. We recommend this book strongly to the general reader as well as to the scientific man. Like a great many astronomers of this day and age Professor Frost leans in his philosophic thinking towards a vaguely mystical sort of deism, which we fear will be somewhat unsympathetically viewed by the younger generation of hard-boiled, wholly materialistic biologists.

THE CONQUEST OF A CONTINENT *or The Expansion of Races in America.*

By Madison Grant. Charles Scribner's Sons, New York. $3.00. 8⅝ x 6; xv + 393; 1933.

The thesis of this history of the United States is that Protestant Nordics were not only the best immigrants this country ever received, its best soldiers, and its best citizens but they were so far in the majority during its colonization and up until the Civil War that they alone are the founders of the nation. No other group has made any significant contribution of a beneficial sort to our culture according to Grant, and it is the duty of Protestant Nordics to take immediate steps to preserve their supremacy, among other things by putting a stop to all further immigration, deporting as many aliens as possible, and putting into effect a number of eugenic proposals. The plan of the book is to classify each group of immigrants according to its racial composition, and to trace the movements of its members and their descendants as they migrated from state to state, and to present a racial survey of the 48 states and of the Latin-American countries to the south. There are about a dozen maps, a bibliography, and an index. Every professional flag-waver will want a copy.

FLIGHT INTO AMERICA'S PAST. *Inca Peaks and Maya Jungles.*

By Marie Beale. G. P. Putnam's Sons, New York. $3.50. 9¼ x 6¼; xv + 286; 1933.

A travel book of considerable interest, by an amateur archeologist. Mrs. Beale writes most entertainingly of her trip, mostly by airplane, from Buenos Aires across the Andes to Santiago and then into the land of the Inca. One never ceases to marvel that Cuzco, the sacred city of the Inca, situated high in the Andes and seemingly almost inaccessible to the European invaders, should have become a Spanish town within fifty years of Columbus' great discovery. Inca rule was paternalistic. Close communication was kept up throughout the vast area by well built foot ways. It is said that fish from the ocean could be delivered in Cuzco in twenty-four hours. Now by train it takes fifty or more. The author's interest in early Peruvian history led her to visit many places which disclose the high development of Inca civilization and the superimposed Spanish culture. After Lima she went to Guatamala and Yucatan and visited Mayan ruins.

Her book is profusely illustrated, mostly with her own photographs, which are excellent. A bibliography is included but there is no index.

FROHE LEBENSARBEIT. *Erinnerungen und Bekenntnisse eines Hygienikers und Naturforschers.*

By Karl B. Lehmann. J. F. Lehmann, München. 4.50 marks (paper); 6 marks (cloth). 8⅛ x 5¼; 328; 1933.

Karl Bernhard Lehmann, one of the pioneers in the movement of public health and hygiene in Germany and one of the founders of modern bacteriology, offers us in this book the story of a long life, spent in arduous yet joyous labor. He tells us of his happy school-years in Zurich during the sixties and seventies of the past century; of his years of apprenticeship under Pettenkofer and Koch in Munich and Berlin, and of his 45 successful years as Professor of Hygiene in the medical faculty of the University of Würzburg. Professor Lehmann is far removed from being a mere reporter. There is not a 'dry' page in the whole book. He gives us exquisite and telling character sketches of his many friends and co-workers, and fine descriptions of the countries he lived in or visited. Furthermore, he defines his position with regard to public health, scientific investigation, education, literature, art, politics, the state and destiny of his country, and religion.

It is, in short, a most refreshing and stimulating book, filled with wisdom and grateful optimism.

THE GREAT DOCTORS. *A Biographical History of Medicine.*

By Henry E. Sigerist. Translated from the German by Eden and Cedar Paul. W. W.

Norton and Co., New York. $4.00. 8⅝ x 5½; 436; 1933.

The sub-title indicates the contents of this extremely interesting book, which is a translation from the second German edition. The great doctors are those whose creative work or teachings have had an important part in the evolution of medicine. Fifty-three names (excluding those linked with mythology) are in the list, beginning with Hippocrates and ending with Osler. Briefly but vividly, the lives and works of each of these is in review and the part that each one played in furthering the progress of medicine. Excellent reproductions of portraits are included in the work; also a bibliography of the more important general treatises on the history of medicine and kindred topics, and special works on great doctors. The volume is indexed.

THE BANTU TRIBES OF SOUTH AFRICA. *Reproductions of Photographic Studies. Vol. II, Section III, Plates LIII–LXXVIII. The Suto-Chuana Tribes. Sub-Group III. The Southern BaSotho. With an Introductory Article on the Southern BaSotho and Descriptive Notes on the Plates, by G. P. Lestrade, and a Bibliography of the Southern BaSotho, by I. Schapera.*

By A. M. Duggan-Cronin. Deighton, Bell and Co., Cambridge. 21 shillings. 11½ x 8½; 24 + 26 plates; 1933 (paper).

Section III of Volume II of this valuable anthropological study, previous sections of which have been noticed in earlier numbers of this REVIEW, contains a short introductory article on the southern BaSotho, a bibliography of 10 pages, and 26 excellent photographs showing the physical type of the people, as well as their dress, architecture and customs. Under the guidance of an unusually enlightened group of missionaries who have preserved what was good in the old and adapted it towards the new, native writers have been encouraged to produce "works of a literary nature, of outstanding merit among the literary productions of the modern type among the South African Bantu."

THE CHILD, THE FAMILY AND THE COURT. *A Study of the Administration of Justice in the Field of Domestic Relations. General Findings and Recommendations. U. S. Department of Labor, Children's Bureau Publication No. 193 (revised edition).*

By Bernard Flexner, Reuben Oppenheimer, and Katharine F. Lenroot. U. S. Government Printing Office, Washington. 10 cents. 9⅛ x 5¾; vi + 100; 1933 (paper).

This report recommends the nation-wide establishment of only one type of court to exercise jurisdiction over all cases directly or indirectly regarding children. This court would take the place of the present juvenile courts, family courts, etc., and also extend its activity to include the work now done by the humane societies, social agencies, etc. This consolidation of judicial power is proposed especially to avoid the overlapping of jurisdiction frequently observed in the cases dealt with by these courts and agencies.

OUR FOREFATHERS. *The Gothonic Nations. A Manual of the Ethnography of the Gothic, German, Dutch, Anglo-Saxon, Frisian and Scandinavian Peoples. Volume II.*

By Gudmund Schütte. The Macmillan Co., New York. $9.50. 9 x 6¼; xvi + 482 + 20 plates; 1933.

The promised second volume of this excellent series on ethnic groups is now ready. The first volume was noticed in Volume 5 of this REVIEW. This part gives accounts of individual Gothonic tribes (Germanic nations) under the same subject headings as were used in the first volume for the Gothonic nations as a whole, —at least, as far as is possible. This is a detailed and scientific study but it is full of interesting details, such as the seven reasons why England came to be called England rather than some name based on the Saxon element in the population. The descriptions of the primitive architecture of the various tribes are also interesting to the layman.

THE HAND OF MAN. *A Practical Treatise of the Science of Hand Reading Dealing in Detail with its Psychological, Sexual, Superstitious and Medical Aspects.*

By Noel Jaquin. Faber and Faber, London. 12s. 6d. net. 8¾ x 5½; 268; 1933.

New and profitable horizons are here disclosed for the practitioners of the ancient art—pardon! science—of palmistry. It is possible by careful reading of the hand to diagnose the physical ills of an individual, so the author says. For example, diagnosis of cancer in its early stages, or even before it appears, is evidently child's play for Mr. (or is it Professor?) Jaquin. Notwithstanding his great ability he is really modest. There is, though, brief mention of cases in which the physicians had failed at first and only following the hand reading was the true diagnosis made. We sympathize with the poor physicians. How is it possible for them to make a diagnosis when they have not the knowledge acquired through palmistry?

IN WILD NEW BRITAIN. *The Story of Benjamin Danks, Pioneer Missionary. From His Diary.*

Edited by Wallace Dean. Angus and Robertson, Sydney. 6 shillings net. 7¼ x 4¾; xi + 293; 1933.

The Reverend Mr. Benjamin Danks and his wife gave eight years of their youth in the attempt to convert the natives of New Britain to Methodism. From 1875 to 1886 they lived and worked in that savage country and here are recorded their hardships and achievements. One cannot but admire their fortitude and that of all those dedicated to such a cause.

There are a few interesting accounts of local customs, mention of conflict with traders, but in style and viewpoint the book is strictly ecclesiastical and intended to fire missionary zeal in those of the same faith and profession.

THE DIFFUSION OF CULTURE.

By G. Elliot Smith. Watts and Co., London. 7s. 6d. net. 7¾ x 5; x + 244; 1933.

In this book the arch protagonist of the diffusion of culture from a single center, with Egypt as "the pioneer in the invention of civilization," makes a vigorous endeavor to prove the soundness of his position from the very evidence provided by the writings of the antagonists of this theory.

THE EUGENIC PREDICAMENT.

By S. J. Holmes. Harcourt, Brace and Co., New York. $2.00. 8 x 5¼; xi + 232; 1933.

This is an elementary exposition of the principles and aims of eugenics and the genetic facts from which they are derived. In form and content it differs very little from the general run of propagandist literature on the subject.

ARCHIV FÜR BEVÖLKERUNGSWISSENSCHAFT (VOLKSKUNDE) UND BEVÖLKERUNGSPOLITIK. *IV. Jahrg., Heft 1.*

Edited by Kurt Vowinckel. S. Hirzel, Leipzig. 10 marks per volume of six numbers; 2 marks, single copy. 9⅜ x 6⅝; 80; 1933.

We welcome this journal dealing with population problems and recommend it to our readers interested in the subject.

JUVENILE-COURT STATISTICS, 1931. *Based on Information Supplied by 92 Courts. Fifth Annual Report. United States Department of Labor, Children's Bureau Publication No. 222.*

U. S. Government Printing Office, Washington. 10 cents. 9⅛ x 5¾; ii + 62; 1933 (paper).

The report for the year 1931 presents much the same situation as that for the previous year (*cf.* this REVIEW, Vol. VIII, p. 114).

THE COUNTY AS AN ADMINISTRATIVE UNIT FOR SOCIAL WORK. *United States Department of Labor, Children's Bureau Publication No. 224.*

By Mary R. Colby. U. S. Government Printing Office, Washington. 5 cents. 9⅛ x 5¾; v + 48; 1933 (paper).

ZOÖLOGY

BELAUSCHTES LEBEN. *Kleine Kreatur in Wasser, Busch und Halm.*

By Karl O. Bartels. Hugo Bermühler, Berlin-Lichterfelde. 3.90 marks (paper); 4.80 marks (cloth). 10¼ x 7¾; xi + 182; 1934.

Here are 120 pages of extraordinary reproductions of photographs of small animals shown in various stages of active life in natural habitats. The reproductions are technically excellent, giving full force to the beauty of the subjects. The phases of behavior are emphasized by serial pictures such as illustrate the stages of the engulfment of a minnow by a coelenterate, the emergence of a damsel fly, the mating of mantids in which the male is finally eaten by the female, a caterpillar spinning its cocoon, and many others equally interesting. The pictures are arranged so that biological forms take a related order. Each picture has a title and descriptive notes accompanying it. After the pictures there follow about fifty pages of text in which are given interesting comments on the biology of the general classes. The pictures representative of the class are also discussed in the order in which they are arranged in the first part of the book. An alphabetical index is given last. This book will be valued by the scientific biologist as well as by the esthetic nature lover, and it will probably attract many who are habitually indifferent to the less obvious occurrences in nature.

DIPTERA OF PATAGONIA AND SOUTH CHILE. *Based Mainly on Material in the British Museum (Natural History). Part IV. Empididae.*

By J. E. Collin. British Museum (Natural History), London. 15 shillings net. 8½ x 5⅝; viii + 334; 1933.

The first volume of this series by Alexander, noticed in Volume VI of the REVIEW, gives a brief description of the collecting trip where specimens described here were gathered. The collecting was done by F. W. Edwards of the British Museum and R. C. Shannon of the Bacteriological Institute of the National Department of Hygiene, Argentina. There were about 30,000 specimens of Diptera taken which eventually will be described in seven volumes. This section by Collin, although Part IV, is the second to be completed. There were 247 species of Empididae represented in the collection, of which 198 are new to science. All these and some Empididae from other collections made in the same area are included in the detailed taxonomic description. There is an index.

> There appears to be a general tendency for the Empid fauna of any distinct faunal region to develop marked peculiarities of its own, and the Patagonian fauna is certainly no exception, but it will be gathered from the information here given, that, on the whole, it shows a distinctly greater resemblance to the fauna of the South Australian region than to any other.

REPTILES OF THE WORLD. *The Crocodilians, Lizards, Snakes, Turtles and Tortoises of the Eastern and Western Hemispheres. New Revised Edition.*

By Raymond L. Ditmars. The Macmillan Co., New York. $5.00. 9½ x 6; xx + 321 + 89 plates; 1933.

A new edition, revised and containing much new material, of a work which has been widely accepted as standard in the study of reptiles (first edition 1910). The nomenclature has been completely brought up to date and the text enlarged to include all recent important discoveries. The work, however, departs considerably from the hand-book type. The author presents in popular manner a general survey of the reptiles of the world and includes many of his own methods in capturing, feeding and treatment of animals in captivity. The 89 excellent photographic plates collected at the end of the volume are valuable for identification purposes. There is an index.

GULLIVER IN THE BUSH. *Wanderings of an Australian Entomologist.*

By H. J. Carter. Angus and Robertson, Sydney. 6 shillings. 7¼ x 4¾; v + 234; 1933.

Gulliver, in the person of the author, is an Australian entomologist and natural historian who writes of his many experiences while rambling over the Australian continent. A chapter (or more) is devoted to each of the divisions of the Commonwealth including the island of Tasmania. The author stresses his personal experiences while collecting in the various regions and gives the reader many interesting annotations about insect life. The book is of interest to the American reader since it gives a familiar insight into the all too unfamiliar Australia. Mr. Carter does not hesitate to tell of his companions and various people met with on his travels, which frequently adds zest to the reading. Some readers will find many of the references to insect life too anthropomorphic to suit their taste.

BIOLOGY OF BRACHYMERIA FONSCOLOMBEI (DUFOUR), A HYMENOPTEROUS PARASITE OF BLOWFLY LARVAE. *U. S. Department of Agriculture Technical Bulletin No. 365.*

By Raiford A. Roberts. U. S. Government Printing Office, Washington. 5 cents. 9 x 5⅞; 21; 1933 (paper).

Brachymeria, a chalcid parasite of blowfly larvae, is carefully studied under field conditions. It is found in Europe, Asia, and North America where it most actively parasitizes larvae of the genus *Sarcophagia*. It readily attacks *Synthesiomyia*, *Phoremia*, *Lucia*, and *Calliphora*, but when it attacks the screw-worm, larvae of *Cochliomyia macellaria* Fab., both insects fail to complete development.

The parasite egg is injected into the host larvae, where, upon hatching, it develops within the maggot. After pupation of the host the parasite completely consumes the pupae and then pupates within the host puparium. Eggs from unfertilized females produce only males, and the sex ratios are frequently irregular in progeny from fertilized females. At Uvalde, Texas, eight generations occur during the year, and about one third of the fly larvae in small field carcasses are infested. The parasite might be useful in control of the blowfly population in general, but as a specific agent against the screw-worm it is not recommended.

MORPHOLOGY OF THE INSECT ABDOMEN. *Part II. The Genital Ducts and the Ovipositor. Smithsonian Miscellaneous Collections, Volume 89, Number 8. (Publication 3219.)*

By R. E. Snodgrass. Smithsonian Institution, Washington. 45 cents (free to public libraries). 9½ x 6¼; 148; 1933 (paper).

A second monograph on the morphology of the insect abdomen by the leading authority on insect anatomy (Part 1. General structure of the abdomen and its appendages). It forms part of a general scheme "to discover the basic plan of arthropod organization that is repeated through the segments, and to see how the special modification in the several body regions of the insect may conform with the structure of a theoretically generalized segment." The author first discusses the general structure of the insect abdomen and the morphology of the gonads and the genital ducts. There follow sections on the ovipositor and associated organs, the ovipositor of Orthoptera, of Hemiptera, and of Hymenoptera. Forty-eight figures accompany the text and a lengthy literature list is given.

THE NIDIFICATION OF BIRDS OF THE INDIAN EMPIRE. *Volume II. Turdidae–Sturnidae.*

By E. C. Stuart Baker. Taylor and Francis, London. 30 shillings net. 8⅞ x 6; vii + 564; 1933.

In this volume the breeding habits and nests of 403 species and subspecies of Passeres breeding in India are described. The material is arranged by families and subfamilies, and includes the thrushes, shrikes, warblers (including the tailor-bird and

the still more remarkable Ashy wren-warbler), goldcrests, bluebirds, orioles, grackles, and starlings. The classification agrees for the most part with that found in the author's earlier volumes on these birds in the *Fauna of British India* series. Although much detailed information is supplied in summary form, Mr. Baker's gift of style makes the book very readable. An index of common and scientific names is provided, but there is no bibliography although much of the descriptive material has been taken from other writers.

THE ECOLOGY OF ANIMALS.

By Charles Elton. Methuen and Co., London. 3s. 6d. net. 6¾ x 4⅛; vii + 97; 1933.

This little book belongs in a series of monographs designed to give brief but authoritative accounts of the present state of knowledge in biological subjects. The author is Director of the Bureau of Animal Population of the Department of Zoology and Comparative Anatomy in Oxford University. Teachers, students and the general reader will find the volume useful in obtaining general information on economic problems, on the scope of animal ecology, ecological surveys, animal interrelations and habits, densities of animal populations and their rates of increase and fluctuations in numbers. A lengthy literature list is given and there is an index.

THE GROWTH OF SOME YOUNG RAPTORIAL BIRDS. *University of California Publications in Zoology, Volume 40, No. 4.*

By E. Lowell Sumner. University of California Press, Berkeley. 10¼ x 6¾; 32; 1933 (paper).

Seven young owls and three young eagles were kept under observation in the laboratory and in the nest during their growth period. Especial attention was given to the development of down and feathers and a number of photographs are given to illustrate the types of plumage and the appearance of the birds. Measurements of body weight, feather length, and lengths of humerus and ulna were made; all of these measurements fall along sigmoid growth curves. It appears that raptorial birds eat proportionately less than passerine birds.

TERMINOLOGY OF TYPES.

By Donald L. Frizzell. The American Midland Naturalist, Vol. XIV, No. 6, pp. 637–668, 1933.

Another earnest attempt to standardize the terminology of taxonomy. A list of 233 terms is appended giving definitions with the authorities for them. By means of different sizes and styles of type used in this list one can tell which terms the author recommends; which he considers less desirable but "available for use;" and which are objectionable. There is a short general bibliography as well as the references pertaining to the definitions.

BUNYIPS AND BILLABONGS. *An Australian Out of Doors.*

By Charles Fenner. Angus and Robertson, Sydney. 6 shillings net. 7¼ x 4¾; xvi + 241; 1933.

An interestingly written series of nature studies on a wide variety of Australian animals, folklore, and curiosities. Many myths concerning natural phenomena are used to create interest. These are ultimately followed to their origin in nature without loss of the feeling of wonderment. The young reader who enjoys exploratory information about natural things will make a delighted discovery in this book, and there is no dearth of ideas that challenge adult curiosity.

OBSERVATIONS ON THE THERMAL DEATH POINTS OF ANASTREPHA LUDENS (LOEW). *U. S. Department of Agriculture Technical Bulletin No. 400.*

By Hugh H. Darby and E. M. Kapp. U. S. Government Printing Office, Washington. 5 cents. 9⅛ x 5⅞; 18; 1933 (paper).

This brief paper is concerned (1) to see whether insect protoplasm is subject to heat coagulation at temperatures similar

to those which affect other animals, and (2) to determine what climatic conditions can be expected to limit or prevent the establishment of *Anastrepha ludens* (a Trypetid fly) in regions as yet uninfested. The authors, on the basis of their data, answer the first question affirmatively.

THE PULSATORY CYCLE OF THE CONTRACTILE VACUOLES IN THE OPHRYOSCOLECIDAE, CILIATES FROM THE STOMACH OF CATTLE. *University of California Publications in Zoology, Volume 39, No. 11.*

By Ronald F. MacLennan. University of California Press, Berkeley. 60 cents. 10¼ x 6¾; 46; 1933 (paper).

A careful study of the cyclic changes undergone by the contractile vacuole of certain ciliate protozoans (the Ophryoscolecidae) shows that the vacuole has three characteristic phases in its cycle, the resting period, systole and diastole. Morphological changes associated with the vacuole and its protoplasmic surroundings are described. A good bibliography is appended.

SUGGESTIONS FOR PHEASANT MANAGEMENT IN SOUTHERN MICHIGAN.

By Howard M. Wight. Department of Conservation, Lansing, Mich. 9 x 6¼; 25; 1933 (paper).

The material in this pamphlet, intended primarily for farmers and other landowners who wish to increase the supply of pheasants, is based on a five years' study of the habits of these birds by the School of Forestry at the University of Michigan. Suggestions, with directions and illustrations, are given for the improvement of roadsides, woodlots, pasture-land, etc., with the breeding habits of pheasants in mind, the planting of food patches, and predatory control.

ANNUAL REPORT OF THE DIRECTOR OF THE MUSEUM OF COMPARATIVE ZOÖLOGY AT HARVARD COLLEGE TO THE PRESIDENT OF HARVARD COLLEGE FOR 1932–1933.

By Thomas Barbour. Museum of Comparative Zoölogy, Cambridge. 9½ x 6; 69; 1933 (paper).

This includes brief reports by the director of the Museum, Thomas Barbour, and by seventeen curators of different departments of the museum, a list of publications (109 titles) issued during the year August 1, 1932 to July 31, 1933, and a brief account of the use of the income of the Museum's invested funds.

WINTER FEEDING OF WILD LIFE ON NORTHERN FARMS. *U. S. Department of Agriculture Miscellaneous Publication No. 159.*

By Wallace B. Grange. U. S. Government Printing Office, Washington. 5 cents. 9⅛ x 5⅝; 12; 1933 (paper).

A discussion of the need and methods for winter feeding to conserve wild life. Organization of campaigns to insure needed food at the right time, the proper type of food for various birds and animals, and the most economical methods of supplying food and winter protection are considered. Several interesting figures are given which show wild birds making use of provided food and shelter.

THE DINOFLAGELLATA: THE FAMILY HETERODINIIDAE OF THE PERIDINIOIDAE. *Reports on the Scientific Results of the Expedition to the Eastern Tropical Pacific, in Charge of Alexander Agassiz, by the U. S. Fish Commission Steamer "Albatross," from October, 1904, to March, 1905, Lieut.-Commander L. M. Garrett, U. S. N., Commanding. Memoirs of the Museum of Comparative Zoölogy at Harvard College, Vol. LIV, No. 1.*

By Charles A. Kofoid and Alastair M. Adamson. Museum of Comparative Zoölogy of Harvard College, Cambridge. $6.50. 12 x 10; 136 + 22 plates; 1933 (paper).

The family Heterodiniidae comprises a number of relatively rare species of the Peridinioidae restricted to warm temperate and tropical seas. They are only sparsely represented in the surface waters and most of the 35 species, of which five are new, described and figured here were taken at 300 fathoms.

THE LIFE HISTORIES AND ECOLOGY OF JACK RABBITS LEPUS ALLENI AND LEPUS CALIFORNICUS SSP., IN RELATION TO GRAZING IN ARIZONA. *College of Agriculture, Agricultural Experiment Station Technical Bulletin No. 49.*

By Charles T. Vorhies and Walter P. Taylor. University of Arizona, Tucson. 9 x 6⅛; 120; 1933 (paper).

A good account of the life history and habits of the jack rabbits, with remarks on the natural enemies, parasites and methods of control.

THE CANADA JAYS OF NORTHERN IDAHO. *Transactions of the San Diego Society of Natural History, Vol. VII, No. 25.*

By Alden H. Miller. San Diego Society of Natural History, San Diego, Calif. 10⅛ x 6⅞; 9; 1933 (paper).

TRANSPOSED HINGE STRUCTURES IN LAMELLIBRANCHS. *Transactions of the San Diego Society of Natural History, Vol. VII, No. 26.*

By W. P. Popenoe and W. A. Findlay. San Diego Society of Natural History, San Diego, Calif. 10⅛ x 6⅞; 14 + 1 plate; 1933 (paper).

MEN AND BIRDS IN JOINT OCCUPATION OF NATIONAL PARKS.

By George M. Wright. The Condor, Vol. XXXV, November 1933, pp. 213–218.

REVIEW OF THE RECENT MAMMAL FAUNA OF CALIFORNIA. *University of California Publications in Zoology, Volume 40, No. 2.*

By Joseph Grinnell. University of California Press, Berkeley. $1.25. 10¼ x 6¾; 64; 1933 (paper).

MAMMALS OF THE POCATELLO REGION OF SOUTHEASTERN IDAHO. *University of California Publications in Zoology, Volume 40, No. 3.*

By Wayne B. Whitlow and E. Raymond Hall. University of California Press, Berkeley. 35 cents. 10¼ x 6¾; 42; 1933 (paper).

BOTANY

RECENT ADVANCES IN THE STUDY OF PLANT VIRUSES.

By Kenneth M. Smith. P. Blakiston's Son and Co., Philadelphia. $4.00. 7¾ x 5¼; xii + 423; 1934.

In the preface the author states that

> The present volume has . . . . been written in the hope that it will serve the dual purpose, first of giving a fairly comprehensive survey of the present position of the knowledge concerning these interesting agents (plant viruses), and secondly of acting as a students' reference book until the progress and correlation of knowledge allow a more comprehensive treatise to be written. For the latter reason, certain subjects have been dealt with in greater detail than is usual in a book of this type.

The volume will be found most useful to those working in this field. The technique of studying plant viruses is described in detail, as well as the diseases they cause. Comparisons are drawn in the behavior of the plant and animal viruses so far as is possible in the present development of knowledge concerning them, and profitable lines of future work are indicated. Each section concludes with a lengthy literature list. The volume is well illustrated and contains author and general indices.

THE PEOPLE'S FORESTS.

By Robert Marshall. Harrison Smith and Robert Haas, New York. $2.00. 8⅛ x 5⅛; 233; 1933.

The author first discusses the great devastation of our forests from the time of the early settlements up to the present and the usefulness of forests as raw material, for soil and water conservation, and for recreational purposes. The latter part of the book is concerned with a discussion of various types of ownership and control of forests and "their effect on the forest, on efficient land use, on the workers, on the consumers and on the dependent communities." In the final chapter is given an outline for a national program of forest conservation. The author is a professional forester who in 1932 collaborated with the Forest Service in the preparation of a comprehensive report on the nation's forests. The book contains a list of references and is indexed.

PFLANZENTHERMODYNAMIK.

By Kurt Stern. Julius Springer, Berlin. 32 marks (paper); 33.20 marks (cloth). 8⅝ x 5⅝; xi + 412; 1933.

Professor Stern makes no claim that his book will be easy reading, but no introduction to thermodynamics is likely to be easy. The first 200 pages are intended to teach biologists enough about thermodynamics to enable them to understand its applications to biology. The second part is a discussion of the thermodynamic aspects of a number of plant processes, permeability, the ascent of sap, respiration and other metabolic processes, electrical phenomena and surface phenomena. The text is clearly written and it is an important contribution to physiological literature. It is well indexed, and in the literature citations it is interesting to note that Americans are well represented.

FORTSCHRITTE DER BOTANIK. *Unter Zusammenarbeit mit mehreren Fachgenossen. Zweiter Band. Bericht über das Jahr 1932.*

Edited by Fritz von Wettstein. Julius Springer, Berlin. 24 marks. 9¾ x 6½; iv + 302; 1933 (paper).

This is the second number of an annual review of botany written in the same fashion, and as successfully, as the *Annual Review of Biochemistry*. The field of botany, not including applied botany, has been very thoroughly covered by seventeen German botanists who discuss the advances made in their respective fields in the year 1932. The bibliographies are extensive and it is worth noting that American work is well represented. It is an indispensable book for every botanical library.

SEX IN THE PLANT WORLD.

By Wilfred W. Robbins and Helen M. Pearson. D. Appleton-Century Co., New York. $2.00. 7⅜ x 5; xii + 193; 1933.

This survey of reproduction in the plant kingdom is written for people without previous scientific training and accordingly technical terms have been strictly avoided and the story has been told in pictures as far as possible. As popular scientific writing goes it is well done; a historical background of the subject is provided and the discoverers of important phenomena are mentioned by name. There is less fanciful language than might perhaps have been expected.

QUANTITATIVE BACTERIOLOGY.

By H. O. Halvorson and N. R. Ziegler. Burgess Publishing Co., Minneapolis. $1.90. 11 x 8½; 64; 1933 (paper).

This book provides tables to aid in the solution of equations to determine the probable density of bacteria by the dilution method, the extent of infestation of insects with viruses or bacteria, or other presence-or-absence sampling problems.

LES ASTRAGALUS DU QUÉBEC ET LEURS ALLIÉS IMMÉDIATS. *Contributions du Laboratoire de Botanique de l'Université de Montréal, No. 24.*

By Jacques Rousseau. Institut Botanique, Université de Montréal, Montreal. 75 cents. 9 x 6; 66; 1933 (paper).

MORPHOLOGY

CONTRIBUTIONS TO EMBRYOLOGY. *Volume XXIV, Nos. 139 to 143. Carnegie Institution of Washington Publication No. 443.*

Carnegie Institution of Washington, D.C. $3.25 (paper); $4.25 (cloth). 11⅝ x 9; iii + 202 + 31 plates; 1933.

The following papers are included in this publication: (1) Development of behavior patterns and myelinization of the nervous system in the human fetus and infant, by Orthello R. Langworthy. This is the concluding report of a series of observations concerning the development of behavior patterns in young animals correlated with one demonstrable step in the maturation of the neuron, and myelinization of the nerve-fiber.

(2) Development of the vagina in the human fetus, by Arthur K. Koff. The conclusion is reached that "the upper part of the vagina develops from the müllerian ducts, while the lower portion, about one-fifth, is formed from the sinovaginal bulbs

which arise from the epithelium of the urogenital sinus."

(3) Development of the thyroid, parathyroid and thymus glands in man, by G. Louis Weller, Jr. A review of the interrelationships existing between the elements of these organs, and a discussion of how each of the glands assumes its characteristic adult location and architecture.

(4) Histological studies of the menstruating mucous membrane of the human uterus, by G. W. Bartelmez. Seventeen specimens, removed at operation, are described. The study includes clinical data, gross examination of the mucous membrane, general description of the microscopic preparations with especial reference to the indications of a preceding pseudopregnancy, details concerning glandular structure, stroma elements and extravasations, blood-vessels and lymphatics.

(5) Early cleavage stages of the egg of the monkey (*Macacus rhesus*), by Warren H. Lewis and Carl G. Hartman. This account is based on four eggs obtained from the monkey (*Macacus rhesus*) colony of the Department of Embryology, Carnegie Institution of Washington. When recovered one of these eggs was in the two-cell stage, two eggs were in the four-cell stage and one in the 16-cell stage. The two eggs in the four-cell stage were incubated to the six- and eight-cell stage.

All of these papers are beautifully illustrated and thoroughly documented.

HISTOLOGY.

By S. Ramón-Cajal. Revised by J. F. Tello-Múñoz. Authorized Translation from the Tenth Spanish Edition by M. Fernán-Núñez. William Wood and Co., Baltimore. $8.00. 9 x 5⅞; xiv + 738; 1933.

A translation of an elementary student's textbook, written by the dean of Spanish histologists, which is widely used in Spanish-speaking universities. It presents a compendium of the investigations of the author and his disciples. The method of instruction differs markedly from that in American schools. During the first year the medical student is given a thorough foundation in cytology, its history and philosophy. The normal histologic topography of the individual organs is then taken up, along with the histo-pathology of the same during the second year. The present volume (tenth Spanish edition) is an almost exact literal translation from the Spanish text, so that the nomenclature, phraseology and system will often appear unusual. It is the translator's hope that the reader will be inspired to investigate Spanish medical literature more deeply. The volume is well illustrated. There is an appendix dealing with method of preparation of materials and a detailed index. Dr. Charles H. Mayo contributes a foreword.

AN INTRODUCTION TO THE STUDY OF THE NERVOUS SYSTEM. *Second Edition.*

By E. E. Hewer and G. M. Sandes. William Heinemann (Medical Books), London. 21 shillings net. 9½ x 7¼; xiv + 147; 1933.

This volume, in its second edition, deals in a compact and logical manner with the anatomy, and to some extent the physiology, of the nervous system. Both the central and autonomic systems are considered. One of the most desirable features of the book is its abundance of several-colored diagrams which should be of assistance in orienting the student with reference to his subject. Another point, worthy of praise, is the highly systematic way in which the subject matter is organized. The volume is an out-and-out textbook and the author has rightly treated the material from just that point of view. The book does not seem to be durably bound and would probably quickly show signs of wear if subjected to the rigors of the laboratory.

THE HISTORY OF STAINING.

By H. J. Conn, with contributions from Lloyd Arnold, A. F. Blakeslee, R. S. Cunningham, S. I. Kornhauser, F. W. Mallory, Eugen Unna. Book Service of the Biological Stain Commission, Geneva, N. Y. $2.00. 8½ x 5½; 141; 1933.

Much of the advance in histology and

cytology during the past 75 years has been due to the staining of the structures examined under the microscope. This book traces the history of the various biological stains and includes portraits and biographical sketches of Sir John Hill, the first known user of dyes in microscopy, Gerlach, the father of the staining method in histology, Rudolph Heidenhain, Paul Mayer, Unna, Ehrlich, Flemming, Belling and Mann. Bibliographies to the various chapters and an index are included.

PHYSIOLOGY AND PATHOLOGY

ARTERIOSCLEROSIS. *A Survey of the Problem. A Publication of The Josiah Macy, Jr. Foundation. Edited by Edmund V. Cowdry. The Macmillan Co., New York.* $5.00. 9¼ x 6; xvii + 617; 1933.

Leading American and European investigators have contributed to this survey of the problem of arteriosclerosis sponsored by the Josiah Macy, Jr. Foundation. Its purpose is to give a clearer perspective of our present knowledge of the disease and indicate which appear to be the more promising directions to follow in future research.

The different aspects and phases of this problem are outlined in the Introduction by L. Anschoff, and fully developed by the individual contributors in the chapters that follow. These include an excellent historical summary by E. Long; the description of the normal anatomy and physiology of blood vessels (E. V. Cowdry), their physical properties (C. Bramwell) and chemical constituents (A. Policard). The studies on the possible etiological factors are discussed in the chapters on the chemical changes observed (H. G. Wells), the influence of race and climate (P. Stocks), that of nutrition (S. Weise and G. R. Minot), of infections (W. G. MacCallum), of heredity (G. D. Williams), and on the relation of arteriosclerosis to hypertension (F. Lange). W. Ophüls considers the pathogenesis in man and therapeutic measures are outlined in the paper by J. Wykoff. Available statistical data are presented by E. Sydenstricker. There are also chapters on the incidence of arteriosclerosis in animals (H. Fox) and results of experimental work (N. Anitschow). The incidence and form which this disease takes in certain regions of the body are discussed by such specialists as J. S. Friedenwald, S. Cobb, D. Blain, H. T. Kassner, and E. T. Bell.

In conclusion, the universal opinion is that the work so far is too insufficient and inconclusive to answer the fundamental question of whether this disease can be avoided or remedied.

HISTORY OF CHINESE MEDICINE. *Being a Chronicle of Medical Happenings in China from Ancient Times to the Present Period. By K. Chimin Wong and Wu Lien-Teh. The Tientsin Press, Tientsin, China.* $7.50. 9½ x 6½; xviii + 706; no date.

A history of Chinese medicine necessarily resolves itself into two parts. The first (pp. 1–123) is concerned with medicine as an "indigenous and mysterious art." This period extends from the ancient or legendary period (2697–1122 B.C.) through the historical or golden period (1121 B.C.–960 A.D.) and the medieval or controversial (961–1800 A.D.). K. C. Wong, Licentiate in Medicine and Surgery, Hong Kong, is author of this section.

The second part of the book (pp. 127–595) deals with the struggles for supremacy between the old and new forces after Western medicine was introduced into China. Wu Lien-Teh, director of Manchurian plague prevention service and of national quarantine service has written of this epoch. He points out that "To introduce bodily the medicine of Europe and America into China without attention either to the traditional background or to the special needs of the masses would be as unwise as it would be unworkable."

Both sections of the volume make extremely interesting reading and will be of great value to the medical historian. Chronological tables are arranged for both parts, bibliographies, and indexes of persons and subjects. The illustrations, especially those in part one, form a valuable feature of the book.

MENTAL EFFORT *in Relation to Gaseous Exchange, Heart Rate, and Mechanics of Respiration. Carnegie Institution of Washington Publication No. 446.*

By Francis G. Benedict and Cornelia Golay Benedict. Carnegie Institution of Washington, D. C. $1.00 (paper); $1.50 (cloth). 10 x 6⅞; 83 + 2 plates; 1933.

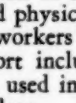
Seven subjects, six men and one woman, all practically normal in every respect except that one very tall man had a basal metabolism averaging 16 per cent below normal, were used in the experiment. The investigators report that

> from a consideration of the various factors measured in our investigation it is concluded that sustained, intense mental effort, consisting chiefly in the multiplication of pairs of 2-digit figures, causes an increase in heart rate, an insignificant, hardly measurable increase in respiration rate, a marked alteration of the character of the respiration, a considerable increase in the apparent total ventilation of the lungs, a small increase in the carbon-dioxide exhalation, a smaller increase (on the average, 4 per cent) in the oxygen consumption and heat production, and a slight increase in the apparent respiratory quotient.

During rest periods between the experiment all factors measured tended to return to original levels.

> During the progress of the four consecutive 15-minute periods of mental effort there was no evidence of any greater effect upon the factors measured during the latter periods than during the first periods.

There was no appreciable alteration in the blood supply to the skin of the head. The conclusion is reached that mental effort *per se* is without significant influence upon the energy metabolism and that its study gives no direct evidence of a satisfactory explanation of the feeling of extreme mental and physical fatigue experienced by mental workers following mental effort. The report includes illustrations of the apparatus used in the experiments and 12 tables of data.



THE GROWTH AND GONAD-STIMULATING HORMONES OF THE ANTERIOR HYPOPHYSIS. *Memoirs of the University of California Volume 11.*

By Herbert M. Evans, Karl Meyer, and Miriam E. Simpson, in collaboration with Alexander J. Szarka, Richard I. Pencharz, Robert E. Cornish and Frederick L. Reichert. University of California Press, Berkeley. $10.00. 12¼ x 9¾; xii + 446 + 14 plates; 1933 (paper).

Fourteen more or less distinct papers make up this magnificent and admirably illustrated quarto. The first four, comprising approximately one-half of the book, deal with the technical details of the preparation, purification and biologic characteristics of the growth and the gonad-stimulating hormones. The second four articles are devoted to studies on the effects of the administration of the hormones to hypophysectomized rats. The ninth paper, subdivided into four parts, contains brief reports of recent experimental work on the relationship between the hypophysis and adrenals. Numbers ten and eleven have to do, respectively, with the influence of the gonad-stimulating extract on the tissue metabolism of immature gonads and the respiratory metabolism of rats tested with the growth hormone. The twelfth and thirteenth sections give accounts of the effect of combinations of extracts on the genital system of hypophysectomized dogs. The last, and from a philosophical point of view the most interesting paper, presents evidence that under the influence of long continued injections of the gonad-stimulating fraction, achondroplastic animals (the dachshund) retain their dysplastic characteristics despite great increase in size. Although it may appear unfortunate to those not technical specialists of endocrinology, the authors have refrained, it seems wisely, from giving a general interpretative summary of their work. References are given at the end of each paper and a subject index for the whole volume is included.

AN OUTLINE OF IMMUNITY.

By W. W. C. Topley. William Wood and Co., Baltimore. $6.00. 9½ x 6½; vii + 415; 1933.

A text-book designed for the advanced student in pathology, bacteriology or hygiene, or more specifically for the preclinical student in medicine. Immunity is defined and considered as that which is

better expressed and understood as resistance. This idea implying variability, the author gives in the second chapter typical statistical procedures useful in immunological problems.

The classical concepts, theories and terminology of the field are given in a developmental order, and they are evaluated in terms of up-to-date experimental procedure. By elucidating each concept with specific examples a great deal of essential technical detail is got into the text. Further clarity is gained by extensive use of protocols and diagrams. The concept that segregation through heredity contributes to the variability in immunological reactions is conspicuously absent.

In cases where the biological nature of the therapy is not beyond the controversial stage, as with bacteriophage and many other newly proposed techniques, the author takes an optimistic attitude and spares no labor in abstracting the best authorities.

The book is carefully organized with index, chapter sub-heads and topic titles. Each chapter has a summary and an extensive list of references.

ROSE RESEARCH ON LYMPHADENOMA.

Contributors: Sir Thomas Horder, M. H. Gordon, Kenneth Stone, Lawrence P. Garrod, E. R. Cullinan, B. D. Pullinger. William Wood and Co., Baltimore. $7.25. 10⅛ x 7¼; v + 136 + 98 plate figures.

The series of papers presented in this book report the essential findings of the last four years of work of the Rose Research on Lymphadenoma. Considerably over half of the volume is devoted to Dr. M. H. Gordon's studies on the etiology of lymphadenoma or Hodgkin's disease, in which it is shown that the etiological agent is not a spirochete, the tubercle bacillus, or a mycotic organism. On the other hand highly convincing evidence is given which indicates that the true causative agent is a particulate, living microorganism of the type of the larger viruses. Other papers in the book include Sir Thomas Horder's clinical description of Hodgkin's disease; Kenneth Stone's and Lawrence Garrod's studies on the serological and morphological characteristics of the yeasts found in adenomatous glands; E. R. Cullinan's hematological observations of inoculated rabbits and guinea pigs; and B. D. Pullinger's contribution to the histology and histogenesis of the lymphoid tissues. Altogether the book is representative of the highest type of cooperative research. The cytological drawings are examples of both superlative medical art and excellent printing.

THE DISTRIBUTION OF THE CURRENTS OF ACTION AND OF INJURY DISPLAYED BY HEART MUSCLE AND OTHER EXCITABLE TISSUES. *University of Michigan Studies, Scientific Series, Volume X.*

By Frank N. Wilson, A. Garrard Macleod and Paul S. Barker. University of Michigan Press, Ann Arbor. $1.50 net. 10¾ x 8; vii + 59; 1933.

Preliminary reports dealing with this investigation have been published (*Proc. Soc. Exp. Biol. Med.*, Vol. 27, p. 588, 1930, and *Jour. Gen. Physiol.*, Vol. 16, p. 423, 1933) but these papers did not include the discussion of currents produced by injured tissue and the intermediate stages of the mathematical treatment presented here. The starting point of this study is the proposition that the electrical relations of organs surrounded by air, as many physiologists have been content to study them, must differ from the relations within the body because air is a good dielectric. The purpose of this treatise is "to discuss in some detail the laws that govern the flow of electric currents in volume conductors; to apply them to the analysis of certain curves obtained with the string galvanometer by leading directly from the surface of the mammalian auricle and from the injured surface of the turtle's ventricle" and to explain the results in terms of the membrane theory.

THE MODERN TREATMENT OF SYPHILIS.

By Joseph E. Moore. Charles C. Thomas, Springfield, Ill. $5.00 postpaid. 9⅞ x 6¼; x + 535; 1933.

This volume satisfies a great need in medical literature. Written by an outstanding clinician it gives in clear and precise terms the therapeutic measures found most effective in the different types of syphilis. The general practitioner, for whom it is intended, will find its fundamental empiricism a relief from the vagueness of theoretical textbooks. While the author does not neglect the philosophical theories, and, in fact, gives an adequate exposition of them, he emphasizes particularly the practical aspects and derives his conclusions almost wholly from his long experience at the head of one of the largest clinics in the country. The statistics presented to justify these conclusions are impressive, but, in our opinion, would carry greater conviction if the data comprised a larger sample of the vast material collected.

In the human biologist especial interest is aroused by the author's comments on the social and personal aspects of the disease, which really deserve further amplification and should be brought to the attention of the layman.

TRAITÉ DE PHYSIOLOGIE NORMALE ET PATHOLOGIQUE. *Tome I. Physiologie Générale. By L. Ambard, M. Arthus, E. Bachrach, A. Blanchetière, H. Cardot, A. Chevallier, A. Lacassagne, A. Policard, G-H. Roger, J. Verne, F. Vlès. Published under the direction of G.-H. Roger and Léon Binet. Masson et Cie, Paris.* 165 francs. 9⅝ x 6⅜; xvi + 1140; 1933.

It is not likely that this introduction to general physiology will fulfill the expectation of its editor and "enhance the prestige of French science." The collaborators in this enterprise have written with considerable literary skill of the general status of their several fields of knowledge and have pointed out certain unsolved problems but they are rather hazy about just what has actually been found out, particularly when the work has been done outside of France. The best section is a survey of biochemistry by Blanchetière which takes up about half the book, and is the only section accompanied by an adequate bibliography. Besides this, there are general surveys of chemical physiology and physical chemistry, and a number of chapters that seem to have been included because they did not belong in any other of the eleven volumes of this treatise. There is no index.

BEHIND THE DOCTOR. *By Logan Clendening. Alfred A. Knopf, New York.* $3.75 net. 9¼ x 6⅛; xxxii + 458; 1933.

This *histoire romancée* of medicine is excellent and, within its limits, very accurate. The scrupulosity of the author is such that he has added an appendix to indicate the points where he has given free play to his imagination or where the authenticity of the historical source is doubtful. The author's intention is to give the layman an understanding of the discoveries which have contributed to the present state of medical knowledge and practice. To accomplish this in an entertaining manner he considers these discoveries in terms of the individuals whose investigations have directly or indirectly led to them. With rare literary skill he describes their personalities, physical and spiritual, their environments, and the means by which they achieved their goals.

Of the many recent popular books on medical history this is without a doubt one of the best.

LA DUALISME DE LA CONTRACTION CARDIAQUE. *Recherches Expérimentales du Laboratoire de Thérapeutique de l'Université de Liège. By F. Henrijean. Masson et Cie, Paris.* 50 francs. 9¾ x 6¼; xi + 350; 1933 (paper).

In this posthumous publication of the eminent Belgian physiologist are recorded the ultimate theories derived from his investigations on the nature of the heart beat. Special emphasis is placed on the fact that in certain conditions spontaneous

contractions and formation of the rhythmical electrical phenomena of the heart persist after death. Also, experiments on the effects of chloroform, ether, and variations in the quantity of the sodium, calcium, or potassium ions on the cardiac functions as observed with electrocardiograms lead the author to reject the possibility that the myogenic or neurogenic theories alone can explain the character of the cardiac contraction. The complicated picture which he presents cannot be here described but in the reviewer's opinion warrants further investigation.

LES RÉACTIONS DU TISSU PULMONAIRE DANS LA TUBERCULOSE. *Étude Expérimentale et Interprétation. (Substratum Anatomo-Pathologique de l'État d' Allergie).*

By E. Leuret and J. Caussimon. Masson et Cie, Paris. 30 francs. 9¾ x 6¾; iv + 85; 1933 (paper).

This is one of a series of studies on tuberculosis undertaken under the direction of Professor Léon Bernard. Experimental work on rabbits leads the authors to the view that in pulmonary lesions the important factor relative to the outcome is the reaction of the tissues to the causative foreign elements. The elimination of these elements they observe follows a simple scheme. This is evidently not so in human tuberculosis. They explain this departure from the simplicity of reaction on the basis that the follicular lesions are caused by more or less temporary fixation of tubercle bacilli, so that, in the evolution of the disease there is formation of polymorphic lesions due to alternating fixation and elimination.

THE NEW DENTISTRY. *A Phase of Preventive Medicine. Six Lowell Lectures.*

By Leroy M. S. Miner. Harvard University Press, Cambridge. $2.00. 7½ x 4⅞; 219; 1933.

The development of dentistry as a modern science is outlined in an interesting and readable form. Archeological evidence of dentistry is reviewed; the crude as well as clever craftmanship of historical ages is pointed out; and the discussion of the replacement of mechanical dental procedure by a broad knowledge derived from biological research makes up the major part of the book. Although the style is that of the popular lecture, the thoroughly scientific outlook of the author is always evident. The book can be recommended as a worthy appeal for unbiased programs of research in all phases of biology.

LES PRÉMATURÉS. *I. Physiologie du Prématuré, by H. Vignes. II. Étude Clinique et Thérapeutique, by G. Blechmann.*

Masson et Cie, Paris. 20 francs. 7¾ x 5⅛; 166; 1933 (paper).

The physiological inferiority of the premature infant is described by Dr. H. Vignes in the first part of this book. He observes that the probability of survival is dependent upon the degree of prematurity, the absence of birth trauma, and the absence of congenital disease. In the second part, Dr. Blechmann discusses the clinical measures and therapy that aid a normal adaptation to extra-uterine life. It is written in concise style and the review of the literature is excellent.

PROBLÈMES THÉORIQUES ET PRATIQUES DE LA TRANSFUSION SANGUINE. *Dix Leçons: Indications. Groupes Sanguins. Accidents. Technique. Organisation. Hémothérapie. Phylactotransfusion. Immunotransfusion.*

By Arnault Tzanck. Masson et Cie, Paris. 35 francs. 9⅛ x 6⅛; 212; 1933 (paper).

The author appears to have covered pretty thoroughly in this handbook the work of the French on blood transfusion. The material is divided into ten sections covering the ground indicated in the title. It includes a discussion of transfusion from cadaver to living man, and ends with 28 aphorisms. The bibliography of three pages is confined to French items, mostly by the author and his co-workers in the hospitals of Paris.

OUR COMMON ENEMY: COLDS.
By the Editors of "Fortune" in Consultation with Eminent Physicians. Robert M. McBride and Co., New York. $1.00. 6¾ x 4½; 102; 1934.

This little book sums up for the general reader what is known about the causation and treatment of colds. The good old remedy, "rest in bed," still seems to be the best measure, not only to cure a cold, but to prevent its spread to other victims. The book was published too early to mention the encouraging results found by Diehl from the use of codein and papaverin. The second part of the book gives an amusing description of the business of advertising and selling cold remedies.

DIET AND DENTAL HEALTH.
By Milton T. Hanke. University of Chicago Press, Chicago. $4.00. 9 x 6; xi + 236; 1933.

With the financial assistance of the California Fruit Growers Exchange, the author and the Chicago Dental Research Club (an organization of twelve practicing dentists) are able to present in this book convincing evidence that in the majority of growing children gingivitis may be prevented and cured, and dental caries may be arrested and prevented, by the daily addition of one pint of orange juice to an otherwise adequate diet. The book is not well written and includes much that is superfluous; its value is greatly enhanced by the inclusion of a series of beautiful color photographs and an appendix of seriatim observations for a three-year period of the oral status of 400 children.

SYMPOSIUM ON METABOLISM. *Sigma Xi Lectures for 1933. Ohio State University. Ohio State Chapter Sigma Xi, Columbus.* $1.00. 10 x 6¾; 130; 1933 (paper).

T. M. Carpenter contributes two very readable articles, one on the history of the measurement of the gaseous products of metabolism and heat production in man, in which the principles underlying the measurement are explained nicely; and one on the interpretation of such data. J. R. Murlin discusses the work done on carbohydrate metabolism in his laboratory; J. B. Brown reviews fat metabolism briefly; W. C. Rose discusses the nutritional significance of amino acids; E. B. Forbes has a chapter on mineral metabolism; and G. M. Curtis rounds off the collection with a paper principally devoted to the iodine-goiter problem. The whole series makes a convenient introduction to the field for anyone who has had a year or two of chemistry.

STARLING'S PRINCIPLES OF HUMAN PHYSIOLOGY. *Sixth Edition.*
Edited and Revised by C. Lovatt Evans. The Chapters on the Central Nervous System and Sense Organs Revised by H. Hartridge. Lea and Febiger, Philadelphia. $8.75. 9⅜ x 6; xiii + 1122; 1933.

We have already commented (Vol. I, p. 599) on the masterly way in which the whole field of physiology was surveyed by the late Professor Starling. The sixth edition, prepared by Professor Evans, has been thoroughly revised and several chapters have been largely rewritten to keep up with recent developments. In this edition a few literature references, usually to reviews, have been added to each chapter.

LABORATORY DIRECTIONS IN GENERAL PHYSIOLOGY. *Third Revised Edition.*
By E. Newton Harvey and Arthur K. Parpart. Henry Holt and Co., New York. 60 cents. 9¾ x 7⅝; iii + 45; 1933 (paper)

This is the third revised edition of laboratory directions covering the topics: physical chemistry of cells, movement, circulation, and respiration. The directions are clearly worded and the apparatus requirements moderate.

TRAVAUX DU LABORATOIRE DE MICROBIOLOGIE DE LA FACULTÉ DE PHARMACIE DE NANCY. *Fascicule VI.*

Faculté de Pharmacie, Nancy. 9⅝ x 6⅜; 164; 1933 (paper).

BIOCHEMISTRY

MEDIZINISCHE KOLLOIDLEHRE. *Lieferungen 6, 7, 8 und 9.*

Edited by L. Lichtwitz, Raph. Ed. Liesegang and Karl Spiro. Theodor Steinkopff, Dresden. 5 marks each. 10⅜ x 7⅞; Lief. 6, pp. 385–464; Lief. 7, pp. 465–528; Lief. 8, pp. 529–608; Lief. 9, pp. 609–688; 1933 (paper).

Previous sections of this excellent series of papers on the application of colloid research to medicine have already been noticed in these columns. In the present four numbers K. Klinke discusses blood (with a section on thrombosis and embolism, by H. Lampert, and one on the vehicular function of the white corpuscles, by Hermann Bernhold) and lymph; R. E. Liesegang writes on water economy, the kidneys, stomach and intestines; J. Tannenberg treats the blood-vessels; and G. Boehm contributes a paper on muscle.

HANDBUCH DER BIOLOGISCHEN ARBEITSMETHODEN. *Lieferung 423.* Containing following articles: *Methoden zur Untersuchung der chemischen Zusammensetzung von Bakterien*, by Erwin Chargaff; *Bakteriologische Differentialdiagnose*, by Otfrid Ehrismann.

Urban und Schwarzenberg, Berlin. 15.60 marks. 10 x 7; 334; 1933 (paper).

The first paper in this number of the *Abderhalden Handbuch* gives in 57 pages the methods of determining the chemical composition of pneumococci, Friedländer bacilli, the human, bovine and avian tubercle bacilli, hay bacillus, Bacillus Calmette-Guérin, and the diphtheria bacillus.

The second paper on bacteriological differential diagnosis contains instructions for identification, staining and culture. The second paper is indexed and both are documented.

LE PHOSPHORE. *Techniques Chimiques—Physiologie—Pathologie—Thérapeutique.*

By M. Labbé and M. Fabrykant. Masson et Cie, Paris. 55 francs. 10 x 6½; 395; 1933 (paper).

This is a thorough and systematic review of the present knowledge of the chemistry and metabolism of phosphorus and its rôle, physiologically and therapeutically, in certain diseases such as those of the liver, kidneys and bone, anemia, rickets and tetanus. In the lengthy bibliographies provided for each section, French, German and English investigators are fairly evenly represented.

SEX

HUMAN SEX ANATOMY. *A Topographical Hand Atlas.*

By Robert L. Dickinson. The Williams & Wilkins Co., Baltimore. $10.00. 11½ x 9; xiii + 145 + 175 figures; 1933.

This magnificently produced volume is a monument to its author's indefatigable diligence, his love of details, and his skill as a draftsman. It is an encyclopedic atlas of sex in all its aspects, physiological, behavioristic and psychological, as well as anatomical. It is based primarily upon Dr. Dickinson's literally enormous experience as a practicing gynecologist and secondarily upon his wide knowledge of the medical literature of sex in the human species. There are 133 pages of text, divided into nine chapters and a bibliography. These chapters have to do successively with: Purpose and methods; the bony pelvis; uterus, ovaries and tubes; the vagina; the vulva and breast; male genital anatomy; the anatomy of coitus; the anatomy and control of conception; conclusion and program. The remaining and much larger half of the book consists of some 175 plates, arranged on the same plan as the text. All of these plates have

some value; some of them are superb, better than anything hitherto existing; some we regret to say are so crowded and/or so badly arranged as to be merely confusing to the reader.

Altogether this is a remarkable book, that will for a long time be found useful as a reference work. There is a detailed index, and a fairly extensive though by no means complete bibliography. One wonders, to take a single example, at the absence of citation of a book having a similar purpose, point of view and manner of treatment, also illustrated with beautiful if not too precisely accurate quarto plates in color, which appeared over 80 years ago—the *Histoire de la génération de l'homme* by Grimaud de Caux and Martin Saint-Ange.

Dr. Dickinson is an enthusiast and a crusader, trying in his very effective way to make this world a better place to live in by increasing our knowledge about sex. His books are always interesting and stimulating. And no one realizes more clearly than he the incompleteness and deficiencies of his work. Of the present volume he says that it is "a mere sketchbook, a beginning." Some day it will doubtless be followed by a much duller but more systematically thorough treatise. In the meantime every student of the subject will be sincerely grateful to Dr. Dickinson for what he has done.

BIRTH CONTROL IN PRACTICE. *Analysis of Ten Thousand Case Histories of the Birth Control Clinical Research Bureau.*

Text and Tables by Marie E. Kopp. Prepared under the Supervision of a Scientific Advisory Committee. Robert M. McBride and Co., New York. $3.75 net. $8\frac{1}{2}$ x $5\frac{3}{4}$; 290; 1934.

Ten thousand cases from Margaret Sanger's Birth Control Clinic in New York City form the basis for this book. According to the preface the report was prepared under the supervision of a Scientific Advisory Committee by Marie E. Kopp. There is a vast amount of material and detail which does not always make easy and connected reading but is clear and understandable. The book is divided into five sections dealing with sources and methods of collection, sociological and economic factors, physiological factors, indications for the postponement of conception, and a summary.

The statistical treatment is extremely simple, consisting almost entirely of percentages of this and that together with a few averages, medians, and modes. No analysis of the variation of the material in a statistical sense is attempted. There are many tables (81 in fact) given in the body of the text besides 50 master tables in small type given in the appendix. There are many interesting data presented here. Ninety-three per cent are said to have used what they believed to be contraceptives before they applied to the clinic for help. Four per cent had never been pregnant while 6 per cent had practically complete families. The latter group averaged six pregnancies apiece. Sixty per cent of the 10,000 were listed as having "general medical disorders." The results in various respects are not in accord with the data from more carefully and scientifically controlled clinics.

WOMAN'S PERIODICITY.

By Mary Chadwick. Noel Douglas, London. 6 shillings. $7\frac{1}{4}$ x $4\frac{7}{8}$; 228; 1933.

This book begins with a short survey of the customs, beliefs and taboos connected with menstruation and then attempts to trace

where possible the various ways in which these have been handed down to the present day, trying to show how they survive actually in curious superstitions that still obtain among civilized peoples, exercising an even more powerful influence upon their lives from recesses among the deeper structures of the mind of both men and women. From these hiding-places they may be found to originate strange ideas, dreams, phantasies, and symptoms, that assume exaggerated prominence during the menstrual period.

The content and general tone of the book follow in the main the author's earlier work *The Psychological Effects of Menstruation*, noticed with scepticism in this REVIEW (Vol. 8, p. 125).

LA DURÉE DE LA GROSSESSE ET SES ANOMALIES.

By Henri Vignes. Masson et Cie, Paris. 15 francs. 7¾ x 5⅜; 97; 1933 (paper).

An elementary but comprehensive survey of the variability in the duration of pregnancy. The distinguished author is admittedly here preoccupied by the question: "Doctor, when shall I be delivered?" In this review of the many investigations on the subject he attempts to show how absurd it is to make a definite prediction. Moreover, he points out that if the facts do not bear out the prediction, the strain of expectation may have grave psychological effects on the pregnant woman. This observation is expressed with a tone of sarcasm towards the modern woman and illustrated by his own experiences with patients for whom delay interfered with social or other amusements!

SEX HABITS. *A Vital Factor in Well-Being.*

By A. Buschke and F. Jacobsohn. Translated from the German by Eden and Cedar Paul. Emerson Books, New York. $2.50. 7¾ x 5⅜; 204; 1933.

A commendable contribution to rational sex education translated into clear and simple English. The chapters dealing with the anatomy of reproduction are well illustrated and the physiological information is thoroughly scientific. At least half of the volume is given to discussion of the social aspects of sex relative to marriage, heredity, hygiene and many other topics contributory to individual sex sanity.

BIOMETRY

OUTLINES OF BIOMETRIC ANALYSIS. *Part I. Revised Edition.*

By Alan E. Treloar. Burgess Publishing Co., Minneapolis. $1.65. 11 x 8½; 65; 1933 (paper).

This outline was prepared for use in the author's course in Biometric Principles at the University of Minnesota. The method of presentation was developed in large part by the late Professor J. Arthur Harris. The subjects treated are centering constants, dispersion, the normal curve, the binomial series, the χ^2 criterion, correlation and regression, and errors of random sampling. The treatment is clear and the doctrine in general sound, especially in its emphasis on statistical pitfalls. However, the standard deviation of a Poisson series is equal, not to the mean, as the author states, but to the square root of the mean.

MATHEMATICAL FACTS AND PROCESSES PREREQUISITE TO THE STUDY OF THE CALCULUS. *Teachers College, Columbia University, Contributions to Education, No. 572. Published with the Approval of Prof. Clifford B. Upton, Sponsor.*

By William H. Fagerstrom. Bureau of Publications, Teachers College, Columbia University, New York. $1.50. 9 x 5⅞; vii + 68; 1933.

Since one of the important functions of high school mathematics is the preparation of the student for the study of calculus in his college work, the author has analyzed the problems in Granville, Smith and Longley's *Elements of the Differential and Integral Calculus* to see how much of what has been taught the student in high school is actually used in his calculus course. He concludes that part of the time spent on advanced algebra and trigonometry might better be given to analytic geometry.

PSYCHOLOGY AND BEHAVIOR

RACE PSYCHOLOGY. *A Study of Racial Mental Differences.*

By Thomas R. Garth. Whittlesey House, McGraw-Hill Book Co. $2.50. 8 x 5⅜; xiv + 260; 1933.

This is a timely book. It contains much that will be useful to the student of human biology while at the same time it is well within the grasp of the general reader. The author has collected all the results

of a scientific nature on racial differences in mental traits that have been made since 1881. He also includes much of his own work. All the data are tabulated in such form as to be readily comprehended. So much work of a preliminary character remains to be done in this new field that many sections of the book are merely discussions of future lines of profitable study. Three pertinent facts are emphasized in the summary. (1) Selection operates in man as well as elsewhere. "One race of men may profit by the operation of selection, either natural or artificial, while another may not." "That is, through selection one trait may be emphasized in one and not in another, though both possess the trait in common." (2) The races of men are mobile. "What we call races are merely temporary eddies in the history of humankind in which common human traits—at least somatological traits, if not mental traits—have become emphasized. Removal of the barriers causing the eddies causes the emphasis to dissolve in the common racial stream." (3) Nurture changes native traits. "Much of the difference found in the results of studies of racial differences in mental traits is due to differences in nurtural factors and the rest is due to racial mobility, so that one race has a temporary advantage over another." The work contains a lengthy bibliography and an appendix giving a description of experimental and statistical studies in race psychology. There are author and subject indices. R. S. Woodworth contributes a foreword.

HUMAN MENTALITY *in the Light of Psychiatric Experience. An Outline of General Psychiatry.*

By Bror Gadelius. Levin und Munksgaard, Copenhagen. Dan. Cr. 33. 9¾ x 6¾; 620; 1933.

This translation of a revised and enlarged edition of parts I and II, together forming an independent volume, of a Swedish textbook is intended as a general guide to psychology as well as psychiatry. The book opens with a brief historical survey of psychiatric theories and practice and the care of the insane, and a consideration of epistemological viewpoints. Sections follow treating the functional structure of mental life and its morbid changes, the genetic and exogenous causes of mental disease, and treatment. The author's approach is predominantly psychological, and he little more than glides over the morbid anatomy. However, he discusses at length the rôle of the endocrine glands and the vegetative nervous system in mental disorder.

Gadelius apparently has little use for Freudian doctrines and includes a chapter on psychoanalysis merely because

> as I have desired to maintain the extreme importance of psychotherapy in every form of mental suffering, I have found it advisable in view of the great influence exercised by the Freudian doctrines, and the impress of dogmatic one sidedness they have imparted to the theory and practice of medical treatment, to subject psychoanalysis to a critical examination.

Although the book will scarcely be found suitable as a textbook for beginners in this country, it will be valuable to advanced students who wish to become better acquainted with the views of European psychiatrists.

Bibliographies are appended to the separate chapters. The index is not very adequate.

A SURVEY OF THE SCIENCE OF PSYCHOLOGY.

By J. R. Kantor. The Principia Press, Bloomington, Ind. $3.75 postpaid. 9 x 6; xvii + 564; 1933.

Kantor takes the view that all psychological phenomena must be described as part of the activities of an entire organism engaged in preserving a balance among its own numerous processes and in responding to the influences of the environment in such a way as to preserve its totality. Accordingly, his treatment may be classified as organismic. The distinctive feature of the book is the large number of separate fields of human biology which are surveyed in order to provide a basis for a complete description of a psychological organism. There are chapters on human anatomy and physiology, brief reviews of the fundamentals of genetics and development, and in connection with the

discussion of man's ecological relationships there are two chapters on human races and the means by which they can be studied. It is written as a textbook for college students, with the numerous chapter subheadings and subdivisions usually considered appropriate, and it ought to be a good book for college students to be exposed to. In addition to explaining the principles of psychology, the way in which they have been worked out, and the nature of the problems now under study, in an interesting and frequently original way there are a good many provocative introductions to ideas on other subjects as well. For instance, "Free thinking is a rarity. Freedom of thought, in the ordinary sense of the word, merely means that we are not prevented by some particular group from thinking the way some other group does." There are 45 pages of literature references to other textbooks and to recent articles in the standard psychological journals classified according to subject matter, and an excellent index.

THE BLIND IN SCHOOL AND SOCIETY. *A Psychological Study.*

By Thomas D. Cutsforth. D. Appleton-Century Co., New York. $2.50. 8 x 5¼; xvii + 263; 1933.

Dr. Cutsforth, Instructor in Psychology in the University of Kansas, in this book tells us what is wrong with the present system of education for the blind, and gives suggestions for corrective measures. To use a simile of the author's, teachers generally liken a blind child to a six-cylinder automobile with one cylinder missing, rather than one with a five-cylinder engine "organized to function perfectly upon his level of sensory equipment." They therefore think that "his education must not only be education, but must also supply the missing power and also make the car sound as if it really were hitting on six cylinders."

Tests made on children in schools for the blind showed that more often than not the children employ visual concepts when other sensory ones are just as available and much more meaningful to them. Like most pupils the blind are prone to give the answer expected of them by the teacher to make a passing grade. The author, of course, makes no objection to teaching the use of visual symbolism to the blind, so long as no attempt is made to discredit their own meaningful sensory experience.

The thesis that the conventional education given the blind leads to verbal, intellectual and esthetic hypocrisy, as well as to psychological and social maladjustments, is carefully argued, convincingly written and illustrated with numerous case histories. The book is a noteworthy contribution to the psychology of the blind, and should not be neglected by those concerned in their education.

A glossary, bibliography, an appendix of "problems for further study" and an index are provided.

A HUNDRED YEARS OF PSYCHOLOGY. 1833–1933.

By J. C. Flugel. The Macmillan Co., New York. $3.75. 8½ x 5⅝; 384; 1933.

This stimulating and well written book is the first of a series designed to trace the history of the various sciences during the past hundred years. After a survey of psychology as it existed a hundred years ago, a time when its close connection with physiology, and its possible practical applications, especially in education and the study of mental disease, were beginning to be realized, Professor Flugel divides his century into three parts, 1833–1860, 1860–1900, and 1900–1933. In the first of these periods the tendencies already noted continued to develop. The second period is characterized by the growth of experimental psychology and of the evolutionary point of view consequent on Darwin's *Origin of Species*. In the third period "we find psychology embarking on the process of specialization incidental to the growth of new schools, each school having its own peculiar methods and outlook and even to a considerable extent its own peculiar jargon." The description of the various schools and their work gives the reader a clear and vivid picture of the progress of psychology in the past

three decades. In particular, the chapter on Freud is one of the best brief expositions of psychoanalysis that we have found. Flugel emphasizes especially the sociological importance of Freud's work on the super-ego. Only by realizing the archaic and irrational character of the morality that the super-ego imposes can we hope to evolve a more reasonable and humane morality. The book contains a bibliography of ten pages, a chronological table of events in the history of modern psychology, and author and subject indexes.

THE NATURE OF HUMAN CONFLICTS, *or Emotion, Conflict and Will. An Objective Study of Disorganisation and Control of Human Behaviour.*

By A. R. Luria. Translated from the Russian and edited by W. Horsley Gantt. Liveright Publishing Corp., New York. $4.00. $8\frac{3}{8}$ x $5\frac{3}{4}$; xvii + 431; 1932.

Here are presented the results of an experimental psychological investigation on the disorganization and control of human behavior. The ingenious method of routine investigation records, in relation to time and form, the individual motor and speech reactions to spoken stimuli. Thus, according to the author, is reflected "the whole dynamic character of the central neurodynamic process of the attention."

In the first part, on psychophysiology of the affective processes, are illustrated the abnormal reactions associated with various forms of emotion. These lead to the conclusion that "marked disturbances in the motor system occur every time the movements fall directly into the sphere of affect" and this is attributed to the fact that "the cortical apparatus is not in a condition to dominate the masses of excitation in the affect."

In the second and third parts of this volume the author seeks to determine the mode of action and genesis of the conflicting processes which cause the abnormal neurodynamic reactions. This he attempts to determine by the creation of artificial conflicts, observations on hysterical patients, etc., and especially in the study of the development of behavior from childhood to adult age.

This work is an outstanding contribution to psychology.

HYPNOSIS AND SUGGESTIBILITY. *An Experimental Approach.*

By Clark L. Hull. D. Appleton-Century Co., New York. $3.75. $8\frac{3}{4}$ x $5\frac{7}{8}$; xii + 416; 1933.

The primary purpose of this treatise is to make available to the general public the results of a program of experimental research on the problems of hypnosis carried out in Professor Hull's laboratory at Yale over a period of about ten years. In doing this the author has correlated and integrated this work with that of others reported in the literature. The net result is a useful and significant presentation of the whole subject, viewed from a rigidly objective experimental standpoint. The author has no illusion about the extraordinary difficulties and complexities inherent in the phenomena of hypnosis and suggestibility. He says:

> These difficulties are so great that to enter seriously on a program of investigation in this field is a little like tempting fate; it is almost to court scientific disaster. Small wonder that orthodox scientists have usually avoided the subject! Yet each generation may be expected in the future, as in the past, to produce a very few rash souls who will not only risk the dangers of making scientific errors but will also have the courage to brave the semi-superstitious fears of the general public and the uneasy suspicions of their orthodox scientific brethren. It is to them that the present work is really addressed.

The author concludes as the net general result of his study that hypnosis is merely a quantitative upward shift in susceptibility to suggestion, differing only quantitatively and not qualitatively from the normal waking state. Specifically he is of the opinion that no phenomenon can be produced in the hypnotic state that cannot in lesser degree be produced in the normal waking condition.

The book is well organized and written, abundantly and significantly illustrated, and provided with adequate bibliographies and indices.

AN EXPERIMENTAL STUDY OF FACTORS INFLUENCING CONSONANCE JUDGMENTS. *A Study from the Psychological Laboratory of Vanderbilt University. Psychological Monographs, Vol. XLV, No. 2. Whole No. 201. By Eugene G. Bugg. Psychological Review Co., Princeton, N. J.* $1.50. 9⅛ x 6⅛; vi + 100; 1933 (paper).

Although the problem of the consonance of musical tones has been under discussion since the days of Pythagoras there is no general agreement as to the nature of the phenomenon. Some have regarded judgments of consonance as cognitive in character while others have held them to be essentially judgments of pleasantness or unpleasantness. On the basis of his experiments the author of this monograph concludes that comparative judgments of consonance are complex phenomena, which are often influenced by the affective quality of the intervals, but that consonance and affective quality are not synonymous. When subjects were given a single criterion by which to judge the relative consonance of two intervals their judgments in repeated tests were more consistent than when they used several criteria. The gross score obtained for the Seashore Consonance Test is, the author concludes, of little value. There is a bibliography of 31 titles.

THE SUPERNORMAL. *A Critical Introduction to Psychic Science. By G. C. Barnard. Rider and Co., London.* 7s. 6d. net. 8½ x 5½; 256 1933.

"Supernormal," according to the author, "does not imply any more than that the phenomena in question are highly unusual, and take place under conditions and through agencies of whose nature we are ignorant." This book aims to study scientifically what is known "unquestionably" of psychic science. We feel sure that the author has achieved his aim since he explains many of the supernormal events as happening along the fourth dimension—which surely is scientific! In several places and connections, we are warned that the only way to prove supernormal occurrences is by being sympathetic with the medium. Attempting to seize ectoplasm is taboo. The fourth dimension, the subconscious, ectoplasm and other equally *natural* (?) explanations are regarded as sufficient without having recourse to spiritualism.

MODERN MAN IN SEARCH OF A SOUL. *By C. G. Jung. Harcourt, Brace and Co., New York.* $3.00. 8½ x 5½; ix + 282; 1933.

The theme that recurs again and again in this collection of essays by the distinguished Swiss psychotherapist is that, while the purely intellectual fare served up to modern man by science turns out not to be an adequate diet, the neat packages labeled spiritual food which are marketed by the churches prove to be equally deficient in vitamins. Jung is therefore disposed to turn to the mysticism of the East as a richer source of spiritual sustenance. Among other interesting essays are those in which he explains his psychological theory of types and the differences between his viewpoint and that of Freud.

SOME EXPERIMENTS IN FOUR-DIMENSIONAL VISION. *By Geoffrey Hodson and Alexander Horne. Rider and Co., London.* 6 shillings net. 8½ x 5⅜; xxv + 117; 1933.

Mr. Hodson used his faculty of clairvoyant vision in performing five experiments of looking into and through solids, and Mr. Horne did most of the writing-up. The section on results, positive and negative, winds up with the cogent remark:

"What Mr. Hodson did see, however, has greater significance than what he failed to see—to some sceptical minds, perhaps greater significance *because* he failed to satisfy all expectations."

We cannot help wondering what Mr. Hodson would have seen on that face of a cube which was held away from him, without Mr. Horne to ask him such questions as "Can you see the number 13?"

ADOLESCENCE. *Life's Spring Cleaning Time. By Beverley R. Tucker. The Stratford Co., Boston.* $1.25. 7⅜ x 5; vii + 121; 1933.

This little volume is arranged as a guide for parents, teachers and all those who are interested in the adolescent. Essentially a handbook, it gives the reader a comprehensive appreciation of the perturbations which beset youth at this period. No cures are prescribed for the abnormal individual but those cases requiring the attention of a psychiatrist are indicated. The author is Professor of Nervous and Mental Diseases at the Medical College of Virginia. The book has no index.

DE OMNIBUS REBUS ET QUIBUSDEM ALIIS

THE LIMITATIONS OF SCIENCE.

By J. W. N. Sullivan. The Viking Press, New York. $2.75. 8⅛ x 5⅜; v + 307; 1933.

Present day science, Mr. Sullivan concludes, being concerned only with the metrical aspects of phenomena, does not give a complete account of the universe. Biology and psychology in particular have not yet developed concepts adequate to their most important problems. Purpose and values are left out of their subject matter, although science itself is inspired by the value of the disinterested search for truth.

It is very probable, as Whitehead maintains, that the notion of particle will have to be replaced by the notion of organism. In order to avoid a break of continuity the notions of physics will have to be enriched, and this enrichment will come from biology. We can look forward to a further synthesis. The science of mind, at present in such a rudimentary state, will one day take control. In the service of the principle of continuity its concepts will be extended throughout the whole of nature. Only so will science reach the unity towards which it is aiming, and the differences between the sciences of mind and matter, in their present form, will be seen to be unreal.

LA SCIENCE FRANÇAISE DEPUIS LE XVII[e] SIÈCLE.

By Maurice Caullery. Armand Colin, Paris. 10.50 francs. 8¼ x 4⅞; 215; 1933 (paper).

This excellent brief history of French science since the days of Descartes was originally delivered as a series of lectures at the Museum of French Art in New York. Although himself a biologist, Professor Caullery does not neglect physics and chemistry and their technical applications. The essentially positive character of the French mind, he concludes, has saved it from the tendency to construct grandiose edifices of theory upon a slender foundation of facts so characteristic of German science, but has sometimes discouraged the formation of working hypotheses that might have led to new lines of experiment. There is a bibliography of four pages and an index of names.

THE ROMANCE OF RESEARCH.

By L. V. Redman and A. V. H. Mory. The Williams & Wilkins Co., Baltimore. $1.00. 7¼ x 5; x + 149; 1933.

In this number of the *Century of Progress Series* two industrial research chemists trace the dependence of our modern material culture on research in physics and chemistry. In these days of technological unemployment there is a growing feeling that the changes brought about by research are in danger of wrecking our social structure. The authors, however, conclude that what is needed is not less research in the physical sciences but more research in the social sciences.

LA PHILOSOPHIE SCIENTIFIQUE. *Vues Nouvelles sur ses Buts et ses Méthodes. Actualités Scientifiques et Industrielles XLIX.*

By Hans Reichenbach. Translated from the German by Ernest Vouillemin. Hermann et Cie, Paris. 10 francs. 10 x 6½; 42; 1932 (paper).

This interesting book deals briefly with the effect upon philosophy of modern scientific research. Kant's conclusion that space and time are mental categories antecedent to experience goes into the discard along with final causes and vitalism. Statistical regularities replace causal connections, and this change may eventually lead to the solution of the old problem of free will.